THE DISPERSAL OF THREE MISTLETOE SPECIES BY BIRDS IN THE LOSKOP DAM NATURE RESERVE

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The mistletoe species Tapinanthus leendertziae, T. natalitius and Viscum combreticola and their avian dispersal agents were studied in the field during February 1977 - May 1978. The study was carried out in seven different plant communities. Year-round surveys were made of the reproductive phenology of the mistletoes. Aspects of pollination and germination of mistletoes were investigated. The birds visiting mistletoe plants were studied with respect to the rate at which they removed fruit and the way they dealt with mistletoe seeds. The diet of the Yellowfronted Tinker Barbet Pogoniulus chrysoconus, the main dispersor of the seeds of the mistletoes, was studied. Comparisons are made between mistletoes and their dispersal agents in savanna and forest biomes in South Africa, and the dispersal of mistletoes by birds in other continents of the world is reviewed.

Plate 1. Yellowfronted Tinker Barbet bringing food to nestlings
(Courtesy Peter Steyn)

Plate 4. Fruit of T. leendertziae (left) and T. natalitius (right)

1 cm

Plate 5. Fruit of Viscum combreticola

1 cm

Plate 2. Populus alba tree parasitized by tens of individuals of Tapinanthus leendertziae, along the Olifants River just outside the Loskop Dam Nature Reserve

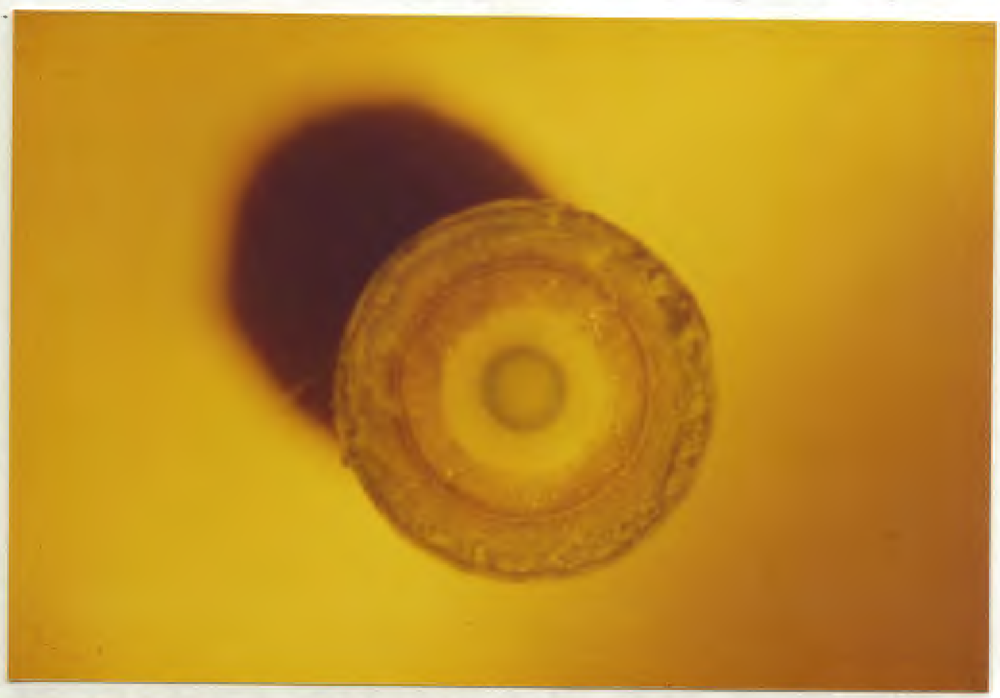


Plate 3. Cross-section through not-fully mature fruit of Tapinanthus natalitius 1 cm

CONTENTS

1. INTRODUCTION

Mistletoes are a world-wide group of plants comprising about 1300 species (Barlow 1964), nearly all of which are hemiparasitic shrubs growing on tree branches. Apart from the genus *Arceuthobium* and a few other species, all mistletoes are distributed by animals, mostly birds (Kuyt 1969).

The consumption of mistletoe fruit by the Mistle Thrush *Turdus viscivorus* was noted by Theophrastus some 300 years B.C. (Ridley 1930), and the Roman Plautus (in *ca*. 254 A.D.) was responsible for the saying: *Turdus ipse sibi cacat malum* (the thrush prepares his own misfortune), referring to the use of birdlime (prepared from mistletoe fruit, distributed by the Mistle Thrush) to catch these birds (Kuyt 1969). However, it was not before the end of the 18th century that mention was made of birds eating mistletoe fruit in Africa south of the Sahara (Thunberg 1795). Since Thunberg, very little information has been published, apart from scattered notes, on mistletoes and birds in Africa, in spite of the fact that about 250 species of mistletoes occur in the region (about 240 species in tropical Africa (Sprague 1913) to which several southern African mistletoes can be added). These notes suggest that tinker barbets (*Pogoniulus* spp.) are particularly connected with the dispersal of African mistletoes.

Bews (1917) pointed to the lack of detailed information on the feeding habits of South African birds, particularly in relation to the dispersal of plant seeds. J.F.V. Phillips (1924, 1926*a*, 1926*b*, 1927, 1928, 1931), working in the Knysna forests, apparently was the first and, until now, the only scientist, to investigate and report on the role of fruit-eating birds in the dispersal of South African plants in detail. Papers on several South African fruit-eating birds have been published, but they make little, if any, reference to the actual roles that the birds play in the dispersal of seeds (Ranger 1950; Skead 1950; Rowan 1967, 1969; Oatley 1970). Furthermore, little is known of the adaptive features of South African mistletoes (and bird-dispersed plants in general) related to seed dispersal by birds, except for some information in the papers by E.P. Phillips (1920), on structural adaptations for dispersal (including dispersal by birds) in several fruits and seeds of South

African plants, and Liversidge (1972), whose study covered the reproductive seasons of selected plant species (including Viscum capense) whose fruit was eaten by Cape Bulbuls Pycnonotus capensis near Port Elizabeth.

During 1976 I carried out a pilot project involving a study of aspects of the dispersal of two mistletoe species by birds (Godschalk 1976). The present report encompasses the results of the first detailed study of the dispersal of mistletoes by birds in Africa. My field work was carried out during February 1977 - April 1978 in the Loskop Dam Nature Reserve, Transvaal, which was selected as the study area because: its vegetation is known in detail (Theron 1973); it supports six species of mistletoes of which three are abundant; and, it supports an abundant population of Yellowfronted Tinker Barbets Pogoniulus chrysoconus (Baker 1970).

My main aims were:

1. to investigate those features of mistletoes which are functionally related to seed dispersal;
2. to establish whether, and to what extent, species of mistletoes differ, and how such differences are related to differences in dispersal strategies;
3. to establish which birds are responsible for the dispersal of different species of mistletoes;
4. to investigate the functional behaviour of these birds as dispersors of mistletoe seed;
5. to investigate the feeding behaviour of the Yellowfronted Tinker Barbet, to see to what extent it is dependent on mistletoe fruit;
6. to discern any difference between different plant communities within an area, with respect to the occurrence, reproductive phenology and dispersal of mistletoes, as well as the occurrence of fruit-eating birds.

Aspects of my study are compared briefly with preliminary findings on the role of tinker barbets as dispersors of mistletoes in coastal dune forest at Mtunzini, in Natal, where P.G.H. Frost, of the FitzPatrick Institute, is currently studying the ecological determinants and co-evolutionary consequences of frugivory to selected plants and birds. Finally, I compare the dispersal of African mistletoes with what is known about their dispersal in other continents.

2. A REVIEW OF THE LITERATURE DEALING WITH THE DISPERSAL OF MISTLETOES BY BIRDS IN AFRICA

Comments on the dispersal of mistletoes by birds in Africa are found as scattered notes in the ornithological literature and in a number of books covering African botany in general, but no detailed study of the subject has been made and a synthesis of the literature has not been attempted previously. The present review is restricted to literature for the Afrotropical Region. (Though not all their arguments are equally strong, I think Crosskey and White (1977) have good reasons for their proposal to replace the zoogeographical term "Ethiopian" Region by "Afrotropical" Region, so the latter is used here). The nomenclature of the southern African Loranthaceae, particularly *Loranthus*, has been revised completely by D. Wiens (in press, *The Flora of Southern Africa* 10(1)) whose arrangement (see Appendix 1) will be followed here, except where only the generic name is used.

The first person to draw attention to a relationship between mistletoes and the Yellowfronted Tinker Barbet was Ayres (1879) who wrote: "those [Yellowfronted Tinker Barbets] I saw were almost always on or near a species of mistletoe which, during our winter months, is well covered with berries, upon which these birds feed. Having nipped off a berry, the bird, with its head well up, cleverly divides it and discards the fruity shell, when the kernel seems to slip down its throat unawares, and the bird has a comical look, as if astonished at the result". Stark and Sclater (1903) and Priest (1934) repeated this description completely and Mackworth-Praed and Grant (1957, 1962, 1970) and McLachlan and Liversidge (1978) undoubtedly had it in mind when referring to the particular fondness of this bird for mistletoe fruit. Dr. H. Exton (quoted by Layard and Sharpe 1884 and Roberts 1935) also recorded mistletoe fruit as food of the Yellowfronted Tinker Barbet. According to Vernon (1977) the Yellowfronted Tinker Barbet is a "wide-spread resident in mixed wood-land where fruit trees and the parasitic plants *Loranthus* and *Viscum* occurred", in the Zimbabwe Ruins area, Rhodesia. This species was recorded to eat fruit of *Loranthus* and *Viscum* "*zeyheri*" by Anon (1962; though the Yellowfronted Barbet was mentioned, according to Reed MS the Yellowfronted Tinker Barbet was actually meant (M. K. Rowan, pers. comm.)).

The congeneric Redfronted Tinker Barbet Pogoniulus pusillus is also regularly reported to eat mistletoe fruit. Fruit of Tapinanthus kraussianus in Natal is eaten by this species (Wood & Evans 1899), and Evans (1895) reported that it eats the "covering" of the fruit, rejecting the seeds and viscid matter around them by banging the fruit with its beak against a tree, where the seeds adhere with the viscid substance and germinate. Cowles (1959), apparently referring to the Red-fronted Tinker Barbet in Zululand, wrote: "Because they are apparently incapable of passing the seeds [of mistletoe] through their digestive tract they must regurgitate the viscidly coated seeds, which frequently adhere to their beak." He then also referred to the wiping of the beak onto a branch to get rid of the sticky seed and concluded: "their fondness for the fruit and their habit of planting the seeds, makes a most interesting profitable interrelationship, very similar in fact to the role of our own western silky flycatcher [Phainopepla nitens] and its distribution of the desert mistletoe [Phoradendron californicum] from one mesquite tree to another [in Mexico and the South-western United States]". This is the only report actually stating that the birds regurgitate the seeds of mistletoe fruit. Other accounts refer to the wiping of seeds onto branches, but not to regurgitation and therefore it is generally not clear what is actually eaten and what is used as nutrition by the birds. Liversidge (1965) recorded a Redfronted Tinker Barbet inspecting ripe fruit of Viscum rotundifolium in the Addo Elephant National Park. Whittall (1969a), in speaking of the "Tinker Barbet Tricholaema diadematum", referred to a native gunbearer in East Africa who said that "where the droppings of this bird fall on a bough, there the mistletoe will grow". However, T. diadematum is not a Tinker Barbet but is the Redfronted Barbet. Subsequently Whittall (1969b), in referring to his original note, mentioned the Redfronted Tinker Barbet. Apparently he confused the two species, but actually meant to refer to the Redfronted Tinker Barbet (John Williams (of the Coryndon Museum, Nairobi) confirmed that fruit of African Loranthus species were the main food of this bird). In his second note, Whittall (1969b) called attention to the stickyness of the seeds and stated that it has been observed that the birds wipe the seeds off their beaks onto a branch, thereby denying the story of his gunbearer.

The Goldenrumped (or Blackcrowned) Tinker Barbet P. bilineatus and the Moustached Green Tinker Barbet P. leucomystax are the chief distributors of Loranthus and Viscum seeds in the Ngong District near Nairobi, Kenya (Van Someren 1956). The Goldenrumped Tinker Barbet was observed to feed Loranthus fruit to nestlings older than one week (Van Someren op. cit.). Vaughan (1929, 1930; also referred to by Jackson & Sclater 1938) reported that in Zanzibar Loranthus is largely spread by birds, the Goldenrumped Tinker Barbet and the Blackeyed Bulbul Pycnonotus barbatus [P. tricolor] being particularly fond of its fruit. The Goldenrumped Tinker Barbet has also been reported to eat fruit of Erianthemum dregei (Anon. 1963a). Loranthus fruit is reported to be an important item in the diet of the Moustached Green Tinker Barbet (Williams 1963).

Room (1972) often disturbed mixed flocks of birds from clumps of fruiting mistletoes Tapinanthus bangwensis in Ghana, but observed only the Speckled Tinker Barbet P. scolopaceus actually eating the fruit. He referred to the situation in Asia where the seeds are swallowed and then, during defaecation, are wiped from the anus onto twigs. Room (op. cit.) stated that the appearance of the seeds attached to twigs in this way was strikingly similar to what he found in the field in Ghana, thereby implying that tnis method is used in Ghana, too. In a previous paper, Room (1971) stated that the "succulent pericarp" of the fruit is eaten and the seeds are rejected and wiped onto twigs. So probably the condition he mentioned subsequently in his 1972 paper was not the result of tinker barbets, but rather of other species of birds eating mistletoe fruit and defaecating the seeds.

The Blackcollared Barbet Lybius torquatus (Anon. 1963c) and the Pied Barbet L. leucomelas (Anon. 1962) have been reported to eat fruit of Viscum and Loranthus, respectively. Phillips (1928) found that the Knysna Loerie Tauraco corythaix ate the fruit of Viscum capense, V. obscurum and V. rotundifolium, rubbing the seeds onto branches, in the Knysna forests in South Africa. The Grey Loerie Crinifer concolor has been reported to eat Viscum fruit. Watt and Breyer-Brandwÿk (1962) reported that V. verrucosum fruit was eaten by mousebirds. Liversidge (1972) recorded the Cape Bulbul Pycnonotus capensis eating fruit of V. capense. According to Bunning (1977), in the Melville Koppies Nature Reserve near Johannesburg, the fruit of V. rotundifolium apparently attracts certain species of birds. In ensuing correspondence (Bunning in litt. 1977), he confirmed that he observed the Redfaced Mousebird Colius indicus, the Crested Barbet Trachyphonus vaillantii and the Blackeyed Bulbul eating fruit of V. rotundifolium. The Cape Sparrow Passer melanurus and the Masked Weaver Ploceus velatus have been recorded to eat Viscum fruit (Anon. 1963b). The Blackeared Seedeater Serinus mennelli also includes mistletoe fruit in its diet (Skead 1960). Van der Byl (1920) suspected the Blackeyed Bulbul and the Yellow Weaver Ploceus subaureus of spreading Tieghemia quinquenervia near Durban because these birds are very fond of the berries of Celtis africana, the main host of T. quinquenervia in that area. Stresemann (1927, quoted by Heim de Balsac & Mayaud 1930) considered members of the Capitonidae and Musophagidae to be dispersors of mistletoes in Africa.

Probably the first report about birds eating mistletoe fruit in South Africa was made by Thunberg (1795, also quoted by Karsten 1939) who wrote: "The Viscum capense, a parasitic plant, was seen disseminated everywhere on the branches of trees (especially of the Rhus) by means of its berries, which the birds are fond of." Dalziel (1937), in West Tropical Africa, Mason (1972), in the western Cape Sandveld, and Williamson (1972), in Malawi, refer generally to the dispersal of mistletoes by birds but provide no particulars of the species involved or the method of dispersal. The process whereby birds wipe seeds of mistletoes off their beaks onto branches is referred to generally by Marloth (1913), Stoneman (1915), Cythna (1962), Batten and Bokelmann (1966), Compton (1966) and Van Hoepen (1968) in southern Africa. More specifically, this is mentioned for Tapinanthus rubromarginatus and T. natalius ssp. zeyheri (Anon. 1964) and Erianthemum dregei, T. natalius and V. nervosum (Gibson 1975). Pole-Evans (1937) reported that it is surmised that birds eat the "soft outer covering" of the fruit of V. minimum, the smallest of South African mistletoes, and wipe off the "hard seeds" from their beaks onto other plants, but Batten and Bokelmann (1966) pointed out that it has not been confirmed that birds distribute this species. According to Meyer (1969) birds eat the "fruit flesh" of mistletoe fruit and attach the seeds to twigs. In Ghana, Irvine (1961) reported that the seeds of Loranthaceae are "dropped on other trees". Stoneman (1915) and Phillips (1920), possibly misled by the common opinion of the seeds being wiped off, thought that the sticky substance around the seed prevents it from being swallowed. Marloth (1913) and Batten and Bokelmann (1966) mentioned the common belief that the seeds have to pass through the intestines of birds before they are able to germinate, but denied this because germinating seeds in unopened fruit were often found. Schönland (1913), making observations on Erianthemum dregei, apparently denied the role of birds and other animals in the planting of the seeds, and suggested that the fruit "dropped down and were, as it were, caught by the branch to which they were glued by viscine derived from the splitting "berry"."

In conclusion, it can be said that definite mention is made in the literature of a special relationship between certain species of tinker barbets and mistletoes. With regard to the general botanical literature, referring only incidentally to the role of avian dispersors of mistletoe seeds, it is often difficult to establish what is based on actual observation and what is just a reflection of common belief, especially with reference to the method of dispersal.

3. STUDY AREA, METHODS AND MATERIALS

3.1 Study area

The Loskop Dam Nature Reserve, centred on 19°19'E, 25°26'S, covers 12 754 ha in the central Transvaal (Figure 1). An introduction to the history, physiography and biota of the reserve is given in Anon (1960). More particularly, the vegetation is described by Theron (1973) and the avifauna by Baker (1970).

The reserve is situated in Mixed Bushveld or Veld Type 18 (Acocks 1975). This is an extremely heterogeneous veld type. The most common trees are Acacia caffra and Combretum apiculatum. According to Theron (1973), six species of mistletoe occur in the reserve. One of these, Tapinanthus rubromarginatus (Engl.) Danser, I did not see during my study, probably because it occurs in the western part of the reserve (Theron, pers. comm.) which I did not visit. Two other species, Erianthemum ngamicum (Sprague) Danser and Viscum rotundifolium L.f., are uncommon. The study was therefore concentrated on the three remaining species: Tapinanthus leendertziae (Sprague) Wiens, T. natalitius ssp. zeyheri (Harv.) Wiens and Viscum combreticola Engl.

Field observations were made at nine sites (Figure 1), which supported mistletoe in fair numbers. The sites included examples of six of Theron's (1973) plant communities. These communities are:

1. Acacia caffra - Combretum apiculatum - Themeda triandra tree-savanna (hereinafter termed "A. caffra - C. apiculatum") represented at site 2.
2. Acacia caffra - Setaria perennis tree-savanna (hereinafter termed "A. caffra") represented at site 3.
3. Acacia karroo - Setaria perennis tree-savanna (hereinafter termed "A. karroo") represented at sites 4 and 5.

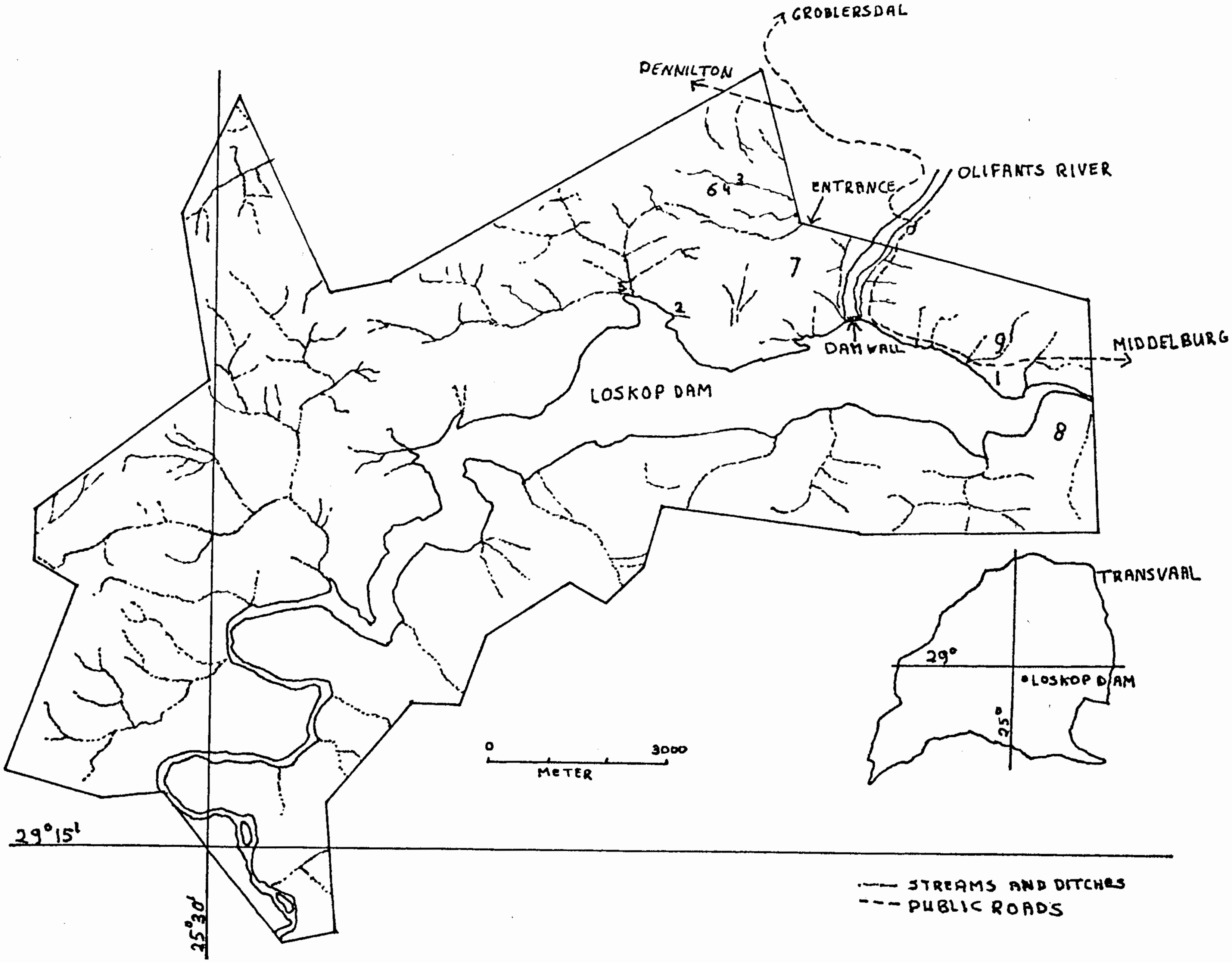

GROBLERSDAL
DENNILTON
OLIFANTS RIVER
ENTRANCE
6
4
3
5
2
7
DAM WALL
9
MIDDELBURG
1
LOSKOP DAM
8
TRANSVAAL
29°
LOSKOP DAM
25°
0
3000
METER
29°15'
25°30'
STREAMS AND DITCHES
PUBLIC ROADS

Figure 1. The Loskop Dam Nature Reserve. The numbers indicate study sites in the different plant communities : 1 = Public Resort ("Camp"), 2 = _A. caffra_ - _C. apiculatum_, 3 = _A. caffra_, 4 and 5 = _A. karroo_, 6 and 7 = _C. apiculatum_, 8 = _Burkea_, 9 = _A. caffra_ - _F. saligna_

4. Combretum apiculatum - Diplorhynchus condylocarpon tree-savanna (hereinafter termed "C. apiculatum") represented at sites 6 and 7.
5. Burkea africana - Ozoroa paniculosa - Loudetia simplex tree-savanna (hereinafter termed "Burkea") represented at site 8. This is a variation of Theron's (1973) Burkea africana - Loudetia simplex community.
6. Acacia caffra - Faurea saligna - Setaria perennis tree-savanna (hereinafter termed "A. caffra - F. saligna") represented at site 9. This is a variation of Theron's (1973) Faurea saligna - Setaria perennis community. Due to road-building activities, I was unable to visit site 9 after August 1977.

A seventh community occurred at the public resort (hereinafter termed "Camp") represented at site 1.

The Camp supported a wide variety of trees, attracting an abundant avifauna. Fig trees (Ficus spp.), of which some had been planted artificially, were common, and Acacia caffra, Combretum apiculatum and C. zeyheri were also well represented. The mistletoes T. leendertziae, T. natalitius, V. combreticola and V. rotundifolium were common in the camp.

The A. caffra-C. apiculatum community was an open-tree savanna on slightly sloping (ca. 4°), south-facing terrain. The most abundant tree was A. caffra, followed by C. apiculatum. Some individuals of the latter species reached a height of 8m. Less abundant trees were C. zeyheri and Dombeya rotundifolia. The three mistletoe species T. leendertziae, T. natalitius and V. combreticola were common. One large C. apiculatum tree was parasitized by at least 25 V. combreticola individuals. A few individuals of V. rotundifolium were also found.

The A. caffra community was a closed-tree savanna on a steep (ca. 24°), south-facing slope. Acacia caffra was the most abundant tree. Combretum molle and Dombeya rotundifolia were less abundant. Tapinanthus leendertziae occurred commonly in the lower part of the slope, whereas V. combreticola was found at higher elevations. Tapinanthus natalitius occurred sparsely. One individual of Erianthemum ngamicum was found.

The A. karroo community was a heterogeneous, heavily-grazed tree savanna on low-lying plains. Acacia caffra, A. karroo, A. nilotica and Dichrostachys cinerea were dominant trees at site 5, where only two Tapinanthus species were found. The four above-mentioned mimosoid species, as well as C. apiculatum and C. zeyheri, were well represented at site 4. All three common mistletoe species (T. leendertziae, T. natalitius and V. combreticola) were represented at the site. Two individuals of E. ngamicum were found.

The C. apiculatum community was situated on moderately sloping (10°-15°), north-facing terrain. It had a rather heterogeneous composition with C. apiculatum being the most abundant tree. Less abundant trees were A. caffra, Lannea discolor and C. zeyheri near site 6, and L. discolor, Dichrostachys cinerea and Sclerocarya caffra near site 7. Few mistletoe plants were found in this community. Apart from the three main species (T. leendertziae, T. natalitius and V. combreticola), a number of E. ngamicum plants were found as well, all on Sclerocarya caffra which was well represented in the community.

The Burkea community was an open-tree savanna with small trees on a slightly sloping (ca. 4°), north-facing plain. Burkea africana was the dominant tree with A. caffra, Ozoroa paniculosa and C. molle as less abundant species. Mistletoes were uncommon and included V. combreticola, a few T. leendertziae and only one representative of T. natalitius.

The A. caffra-F. saligna community was a closed-tree savanna on a steep (ca. 23°), south-facing slope. The dominants, A. caffra, F. saligna and C. molle, were equally well represented at the study site. The mistletoes T. leendertziae, T. natalitius and V. combreticola were common. Some individuals of V. rotundifolium also occurred.

Sites 3, 4 and 6 were located in what I will call the north-eastern valley (hereinafter termed "N.E.V.") which included: the A. caffra community (site 3), occurring on the northern slope; the A. karroo community (site 4) in the trough of the valley; and the C. apiculatum community (site 6) on the southern slope.

3.2 Methods and materials

All hosts of mistletoes encountered were identified. The flowering and fruiting phenologies of mistletoes were surveyed during May 1977 - April 1978. Weekly assessments were made of individually-marked mistletoe plants in each of the seven plant communities. Five classes (O, 1-25%, 26-50%, 51-75%, and 76-100%; scores 0-4, respectively) were used in recording the development of flowering and fruiting stages. The stages were:

Tapinanthus

1. Flower-buds and young flowers
2. Open flowers
3. Very young fruit
4. Unripe fruit
5. Ripe fruit

Viscum

1. Flower-buds and very young fruit (the flowers of Viscum are minute and the early stages of fruit are difficult to discern macroscopically)
2. Unripe fruit
3. Ripe fruit

In addition, several flowering branches of the two Tapinanthus species were "bagged" in an investigation of the role of sunbirds (Nectariniidae) as pollinators.

Some 550 ripe fruits were collected from a T. leendertziae plant growing on an Acacia caffra tree. After storage in deep-freeze for 15 months, the fruit were treated as follows. The exocarp was removed from each fruit. The remaining seed and aril were left together in one group (223 fruit); this sample was called "arillate-seed". In the other group (323 fruit) the aril was removed from the seed. The resulting two samples were called "aril" and "seed" respectively. All three sets of samples were analysed for total water, protein, lipid and fibre contents. Ash and energy contents were determined for "seed" and "arillate-seed" material, and the values for the "aril" were computed from the "seed" and "arillate-seed" figures. All values are expressed on a dry weight basis, unless otherwise stated.

Water content was determined by oven-drying to constant mass at 70°C. Nitrogen content was determined by the macro-Kjeldahl method (Plummer 1971) and the resultant N-value multiplied by 6,25 to get protein content. Total lipid content was determined by Soxhlett petroleum ether extraction (Anon. 1965). The delipidised residue was used for the crude fibre determination and for an amino acid analysis of the aril. The crude fibre content was determined by digestion by acetic and nitric acids, and washing with ethanol and benzene. The residue was weighed and this value was corrected by the ash content value to give the crude fibre content. The energy content was determined by means of a Phillipson microbomb calorimeter, and the remaining residu was weighed and taken as the ash content. The nitrogen-free-extract (NFE) was obtained by subtracting the percentage values of protein, lipid, crude fibre and ash from 100 per cent. An amino acid analysis was carried out on a dry and on a delipidised sample of arils, by means of a Model 121M Beckman amino acid analyzer.

Birds and their behaviour at mistletoe plants bearing fruit were observed in the field with the aid of 7x50 binoculars. All observations were spoken into a tape-recorder. The following records were made: number of species and individuals eating fruit of mistletoes; number of fruit eaten (one fruit was one record); maturity of fruit eaten; duration of feeding bouts and visits; and, the bird's behaviour subsequent to eating and visiting mistletoes. I also counted all trees and mistletoe plants within a radius of 20 m of the tree in which the birds were feeding. All species of fruit-eating birds occurring within a distance of 40 m of the "observation tree" were recorded and their abundance was noted. All dietary items of the Yellow-fronted Tinker Barbet, whenever encountered, were recorded.

Birds belonging to the following species: Blackcollared Barbet, Yellowfronted Tinker Barbet, Crested Barbet, Blackeyed Bulbul, Kurrichane Thrush Turdus libonyana, Olive Thrush T. olivaceus and Cape White-eye Zosterops pallidus, were kept in captivity. They were maintained on apple pieces, oranges, Pro Nutro, meal-worms (Tenebrio molitor) and sugar water. Drinking water was freely available. Fruit of T. natalitius ssp. zeyheri, T. leendertziae, V. combreticola and V. rotundifolium were given to the birds and their responses were observed. Some fruit of locally indigenous plants were also given, to compare the birds' behaviour when feeding on either mistletoes or other fruit. Mistletoe seeds deposited by the birds were used to test whether passage through the alimentary tract affects germination. These seeds as well as other which I "de-exocarped" myself, were planted on a River Bushwillow Combretum erythrophyllum. The seed was considered to have germinated successfully when the hypocotyl had formed a disc on the host.

4. RESULTS AND DISCUSSION

4.1 Botanical aspects

4.1.1 The mistletoes

Mistletoes are hemiparasitic plants which grow on the branches of a variety of host trees, drawing water and mineral requirements from their hosts but synthesizing their own organic substances. Though classified as one family (Loranthaceae sensu lato) in the South African standard botanical literature (Harvey 1862; Sprague 1925; E.P. Phillips 1926; Goossens 1953; Dyer 1975), the modern trend is to separate the mistletoes into two families: Viscaceae and Loranthaceae sensu stricto (Barlow 1964; Kuyt 1969; Tilney & Lubke 1974; Wiens 1978). Both families are represented in southern Africa, containing 55 species in 12 genera (Appendix 1). The following account deals with Tapinanthus leendertziae, T. natalitius and Viscum combreticola, the main species considered in this study.

The two Tapinanthus species are woody, deciduous shrubs. Tapinanthus natalitius , a robustly-built species, sometimes exceeds 1 m (o.d.). Tapinanthus leendertziae is smaller and more finely built. In my study area, leaf buds of both species appeared in August, some five weeks ahead of the flower buds, which started to grow when the leaves were already mature. The leaves had disappeared at the same time as the fruit, in the previous season. Because the reproductive cycle of T. natalitius is longer than that of T. leendertziae, the leafless period of natalitius is about two months shorter than that of leendertziae which extends over four months. Kuyt (1969) reports only two deciduous species of mistletoes, one occurring in Europe and the other in Africa (T. natalitius ssp. zeyheri, Anon. 1964). It is not clear why he did not mention T. rubromarginatus which is described as deciduous, too (vide Anon. 1964). I found T. natalitius as well as T. leendertziae and E. ngamicum to be deciduous, and possibly most South African loranthoids are deciduous in areas with dry winters.

The epigynous flowers of Tapinanthus are bisexual, with the petals completely connate and forming a closed cylinder. The flowers of T. natalitius grow to 6 cm in length and have a long white base, a short yellow throat and a yellowish-green, pointed head of approximately 1 cm in length. The somewhat smaller flowers of T. leendertziae have a dark-red base, a green throat and a short, more or less round, yellowish-green head. Tapinanthus flowers are bird-pollinated (see Section 4.1.4)

Viscum combreticola is an evergreen, dioecious shrub (Sprague 1925). Individual plants are sometimes clumped together, forming a large mass. The leaves are scale-like, and the function of photosynthesis is performed by the dark-green stems. The internodes are compressed and widened to form cladodes which are twisted alternately. Both these characteristics probably improve the plant's photosynthetic ability by maximizing interception of light (Kuyt 1969). The minute, greenish, unisexual, epigynous flowers are probably insect-pollinated, Hymenoptera seem to be the main pollinators of Viscum (Kuyt 1969), and on one accasion I saw a hymenopterid actually probing the flowers.

Mistletoe fruit are pseudocarps, developing from the gynoecium and the surrounding receptacle. Because no ovules are formed, one cannot speak of the production of seeds in the strict morphological sense. A testa is absent. Functionally and ecologically, however, mistletoe fruit can be regarded as one-seeded berries. Because there is no consistency in the anatomical nomenclature for mistletoe fruit, the names used here for the various parts of the fruit are "functional" without pretending any morphological exactness.

The obovoid fruit of T. natalitius reach a length of up to 14 mm. They mature while still in the green stage, but the colour of untouched fruit changes to yellow and finally to dark-red. They become black and very hard when overripe. Because most fruit are eaten in the reen (but ripe) stage, the yellow and red stages are not frequently encountered in the field and therefore their existence is sometimes not mentioned in descriptions of the plant (Anon. 1964; Godschalk 1976). Ali (1931) found the same condition in Loranthus longiflorus in India, because of the high rate of removal of the fruit by birds. Green, ripe fruit are also reported for L. buchneri in Angola (Hiern 1900). The ellipsoid fruit of T. leendertziae, somewhat smaller than those of T. natalitius, are clearly crowned by a persistent calyx. Ripe fruit are bright red and, when overripe, they just fall and rot without becoming black or hard.

The internal anatomies of the fruit of the two Tapinanthus species (Figure 2) are basically similar. The exocarp is usually rather thick and tough when immature, but it becomes thinner and softer during maturation. It encloses the sac-like rest of the fruit. The mesocarp, surrounding the seed completely, consists of an outer aril and an inner viscin layer. The non-sticky pellicle-like aril's main function is to attract dispersors; it is digested by birds. It also separates the very sticky viscin

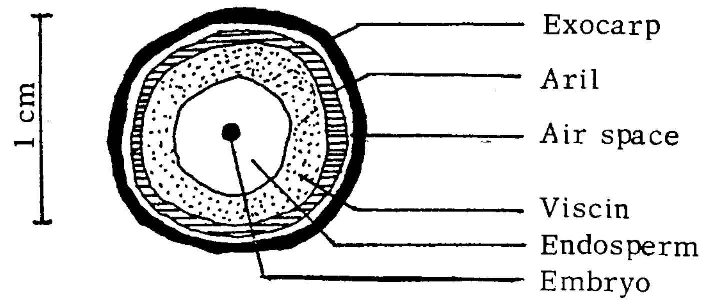


Figure 2. Diagrammatic cross-section through a fruit of *Tapinanthus*

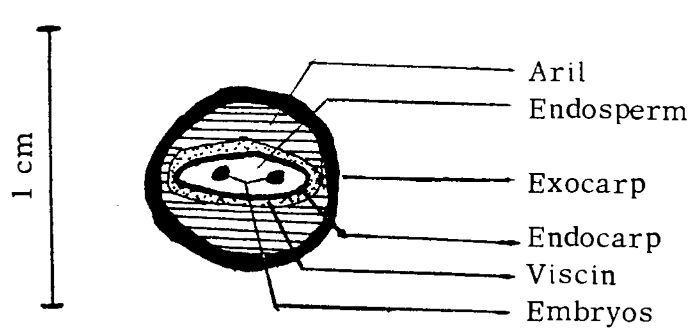


Figure 3. Diagrammatic cross-section through a fruit of *Viscum combreticola*

from the exocarp, and so probably facilitates the handling of fruit by birds. The colour of the aril differs between species. In *T. natalitius* it varies between dark-grey and purplish, and in *T. leendertziae* it is red. In Natal, I found the aril to be orange in *Erianthemum dregei* and light violet in a *Tapinanthus* species. I cannot offer any explanation for an immediate functional significance of these colour differences, because the colours are not visible through the exocarp. Perhaps the colours reflect nothing more than differences in the accumulation of secondary products. In *T. natalitius* the aril can be removed as a whole pellicle, whereas in *T. leendertziae* it breaks readily into pieces. The pinkish-white viscin's main function is to attach the seed to the host branch after egestion by birds. It also mostly causes the seed to stick, after regurgitation, to the beak of a bird, so that the bird is forced to wipe off the seed onto a branch, rather then just dropping it. The viscin may also hold moisture during the first stages of the attachment and aid germination of the seed (Peirce 1905; McLuckie 1923; Gill & Hawksworth 1961; Johri & Bhatnagar 1972, quoted by Kenneally 1973). It may also provide protection for the seed in the alimentary tract of the bird, because the absence of a testa renders the seed susceptible to chemical damage, particularly when seeds are destined for defaecation and hence remain longer in the gut, than when regurgitated. Copious white endosperm is present to provide the seedling with food in its primary stages. Only one embryo is present which is already green (chlorophyll-containing) in the early stages of development. The lack of a testa enhances rapid germination and hence rapid permanent attachment to the host branch. After deposition, the viscin remains rather soft and moist for a considerable peri od; the colour changes from whitish to reddish. Seeds often germinate while still inside the fruit. *Viscum combreticola* has spherical fruit. The fruit has a tough exocarp which in the ripe state is dull orangish-red, becoming greyish-black and hard when overripe. Its internal anatomy (Figure 3) differs in some respects from that of the *Tapinanthus* fruit. The aril is not a definite pellicle but rather a jelly-like, light-orange substance which can fairly easily be separated from the seed. A smaller amount of less sticky, transparent viscin (possibly of a different nature to that of *Tapinanthus* according to the touch of it) surrounds the flattened seed. Soon after deposition, the viscin becomes dry and hard, cementing the seed firmly to the host branch. A definite, very thin, endocarp can be discerned, which may help in the retention of moisture inside the seed after attachment (Gjokic 1896). The endosperm contains some chlorophyll, which may enhance its food-providing function. Normally one or two, but occasionally three, embryos occur in one seed. This polyembryony is possibly of importance in maintaining the dioecious mistletoes in areas where the plants are widely spaced, assuming that plants of both sexes may arise from different embryos within a single seed (Allard 1943, quoted by Gill &

Hawksworth 1961). In monoecious species in which polyembryony occurs (e.g. V. rotundifolium, pers. obs.), however, this cannot be the reason, and cross-pollination might also be of importance.

4.1.2 Hosts of mistletoes

During the course of the study, I recorded 34 host species of mistletoes (Tables 1 and 2). Three of the hosts were mistletoe species themselves and another seven were exotic trees (Table 2). These exotic hosts were found growing outside the boundary of the Loskop Dam Nature Reserve. Table 3 presents information on the relative importance of the host species.

Tapinanthus leendertziae clearly had a wide variety of host species; Acacia caffra being the most important, because it was the most abundant tree in the reserve. Tapinanthus leendertziae was the only species which parasitized exotic trees in fair numbers: an individual Populus alba hosted at least 50 individuals of T. leendertziae which also occurred commonly on Melia azedarach. The species was also found once on T. natalitius and V. combreticola respectively, both times in flowering condition.

Tapinanthus natalitius was mostly restricted to mimosoid host species; A. caffra being the most important host probably because of its abundance. Combretum molle, Pterocarpus rotundifolius and Punica granatum were only once recorded as hosts, and C. apiculatum twice. Tapinanthus natalitius was not found growing on other mistletoes.

Viscum combreticola was mostly confined to Combretum hosts. It was only once found on the other recorded host species. Sometimes heavy infestations of this species occurred, forming large masses of up to 3 m (o.d.). One C. apiculatum tree was parasitized by at least 25 V. combreticola plants. Viscum combreticola plants. Viscum combreticola was found on both Tapinanthus species, though sparsely.

Viscum rotundifolium was found on different host species, and was recorded several times on T. leendertziae.

Table 1. Indigenous hosts of mistletoes in the Loskop Dam Nature Reserve, Transvaal. X indicates records of parasitism. Names and arrangement of trees according to Palgrave (1977)

Host species	Mistletoe species				
	Tapinanthus leendertziae	*T. natalitius* ssp. *zeyheri*	*Viscum combreticola*	*Viscum rotundifolium*	*Erianthemum ngamicum*
A. Host trees					
Mimosoideae					
Acacia caffra	X	X			X
A. karroo	X	X			X
A. nilotica	X	X			
A. robusta		X			
A. sieberana	X	X			
Dichrostachys cinerea	X	X			
Papilionoideae					
Pterocarpus rotundifolius		X			
Euphorbiaceae					
Securinega virosa	X				
Croton gratissimus	X		X		
Anacardiaceae					
Sclerocarya caffra					X
Ozoroa paniculosa	X				
Rhus lancea	X				
R. leptodictya	X				
R. pyroides	X				
Celastraceae					
Maytenus heterophylla	X			X	
Rhamnaceae					
Ziziphus mucronata	X			X	
Combretaceae					
Combretum apiculatum	X	X	X		
C. hereroense	X		X		
C. molle		X	X		
C. zeyheri	X		X		
Ebenaceae					
Euclea crispa	X				
Diospyros lycioides	X				
Oleaceae					
Olea africana			X		
Boraginaceae					
Ehretia rigida				X	
Sub-total	18	9	6	3	3
B. Mistletoes					
Tapinanthus leendertziae			X	X	
T. natalitius ssp. *zeyheri*	X		X		
Viscum combreticola	X				
Sub-total	2	-	2	1	-
Total	20	9	8	4	3

Table 2. Exotic tree-hosts of mistletoes in the surroundings of the Loskop Dam Nature Reserve. X indicates records of parasitism

Host species	Mistletoe species			
	Tapinanthus leendertziae	*T. natalitius* ssp. *zeyheri*	*Viscum combreticola*	*Viscum rotundifolium*
Citrus aurantium (orange)	X			
Ficus carica (cultivated fig)	X			
Melia azedarach (Persian lilac)	X			
Morus alba (mulberry)	X			
Populus alba (poplar)	X			
Prunus persica (peach)	X			
Punica granatum (pomegranate)		X	X	X
Total	6	1	1	1

Table 3. The number of individual trees acting as hosts for 91 individual mistletoe plants of three species surveyed (see Section 3.2) in the Loskop Dam Nature Reserve during March 1977 - April 1978

	Mistletoe species		
Host species	*T. leendertziae*	*T. natalitius*	*V. combreticola*
Acacia caffra	18	24	
A. karroo		2	
Dichrostachys cinerea	1		
Ozoroa paniculosa	1		
Ziziphus mucronata	1		
Combretum apiculatum	1	1	9
C. molle		1	4
C. zeyheri	1		5
Tapinanthus natalitius	1		
Total	24	28	18

Erianthemum ngamicum tended to be confined to Sclerocarya caffra. It was found twice each on Acacia caffra and A. karroo, and eight times on S. caffra.

Erianthemum ngamicum and V. rotundifolium were too uncommon to warrant definite statements on their host specifity, though it appeared as though the former had a preference for Sclerocarya caffra in the study area, which is, however, further discussed in Section 5.1. Viscum rotundifolium is regularly reported to be very unspecific in its choice of hosts (Marloth 1913; Marloth & Drege 1915; Cythna 1962; Tilney 1970; Tilney & Lubke 1974). Viscum combreticola was found to be confined nearly entirely to Combretum species, which agrees with other reports (Cythna 1962; Tilney & Lubke 1974). Tapinanthus natalitius tended to be restricted to mimosoid host species. Tapinanthus leendertziae was highly unspecific. Tapinanthus oleaefolius (of which T. leendertziae formerly was classified as a variety) is reported to be unspecific, too (Tilney 1970).

The causes for the differences in host specifity are not obvious and are most probably to a large extent bound up with the plants' physiology. The relatively wide variety of dispersors of T. leendertziae seed (Table 10), with a broad spectrum of behaviour patterns, might be one contributing factor to the species' wide variety of hosts. Mousebirds were probably to a large extent responsible for the spread of T. leendertziae to the exotic trees all of which, except possibly Populus alba, are fruit-bearing trees regularly visited by these birds (pers. obs.). Differences in the availability of insect food for the dispersor between different host species (found to be important for different host specificity in certain Australian mistletoes (Blakely 1922)) are unlikely to be important for the difference in specificity between T. natalitius and V. combreticola, as the same dispersor is mostly responsible for their spread (Table 10) and the fruiting season of T. natalitius overlaps completely with that of V. combreticola (see Section 4.1.3.1) In certain host species the availability of fruit may have enhanced the spread of mistletoes to these species, depending on their fruiting season (e.g. Securinega virosa, Rhus spp., Ziziphus mucronata, Euclea crispa, Ehretia rigida and certain exotics). Apart from bird behaviour and the fruiting phenology of host plants, the nature of the host's bark and the amount of endosperm available in the mistletoe seed may also play a role in the degree of infestation of different hosts by different mistletoes (Blakely 1922).

Other examples of somewhat host specific South African mistletoes are Viscum crassulae on succulent hosts (Crassula, Euphorbia and Portulacaria) (Marloth &

Dregе 1915; MacOwen, quoted in Sprague 1925), V. minimum on Euphorbia horrida and E. polygona (Engler & Krause 1908; Pole-Evans 1937; Batten & Bokelmann 1966) and V. verrucosum on Acacia spp. (Compton 1966; Tilney 1970; Tilney & Lubke 1974). Highly unspecific species are Erianthemum dregei (Tilney & Lubke 1974), V. capense (Marloth 1913) and V. obscurum (Marloth & Drege 1915).

Hyperparasitism (i.e., one mistletoe species growing on another one) is regularly reported for South African mistletoes, involving loranthoids on viscoids and vice versa (Marloth 1913; Van der Byl 1921; Tilney 1970; Godschalk 1976). I found five types of hyperparasitism (Table 1) of which only V. rotundifolium on T. leendertziae was found regularly. The origin of a hyperparasitic relationship can be ascribed to overlapping fruiting seasons with the dispersor feeding on both species' fruit, carrying the seeds from one species to the other and vice versa.

The best examples of dual parasitism (i.e., more than one species of mistletoe growing on one individual host tree) were a Punica granatum parasitized by T. natalitius, V. combreticola and V. rotundifolium, and a Combretum apiculatum hosting T. leendertziae, T. natalitius and V. combreticola. Two species of mistletoe on one host were found regularly, usually T. leendertziae and T. natalitius or T. leendertziae and V. combreticola.

As the leaves of mistletoes are regularly reported to make good fodder (Marloth 1913; Blakely 1922; May 1941; Coleman 1949; Gill & Hawksworth 1961; Batten & Bokelmann 1966), vegetative mimicry (i.e., resemblance between the leaves of the parasite and those of the host) might provide protection from vertebrate herbivores. This phenomenon is particularly frequent in Australia, but very infrequent in other continents, presumably because of the presence of relatively many arborial herbivores in Australia (Barlow & Wiens 1977). Barlow and Wiens actually state that Wiens was able to find only one suggested case of host mimicry in mistletoes in Africa. In contrast, Tilney and Lubke (1974) wrote that the leaves of Loranthus species in South Africa often resemble those of the host, making them inconspicuous, and refer to a photograph showing Tapinanthus rubromarginatus growing on Protea caffra. The only other reported case for South African mistletoes is Viscum crassulae, the leaves of which strikingly resemble the younger leaves of Portulacaria afra, its main host (MacOwen,

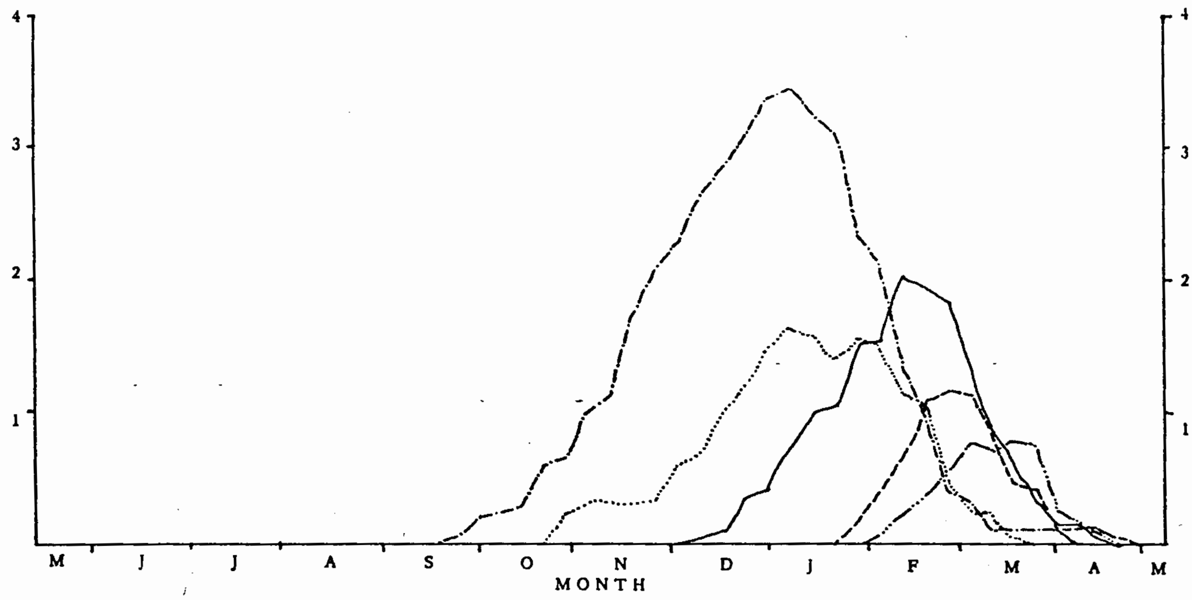


Figure 4. Reproductive phenology of Tapinanthus leendertziae in the Loskop Dam Nature Reserve during 14 May 1977 - 6 May 1978. Different phenological stages: closed flowers (—.—.—), open flowers (..........), very young fruit(———), unripe fruit(– – – – – –), ripe fruit(—.........—). The scores (0-4; see Section 3.2) of all plants of a species, included in the survey, were summed, and divided by the number of plants to get a mean value for each week, which are plotted on the y-axis in Figures 4-8

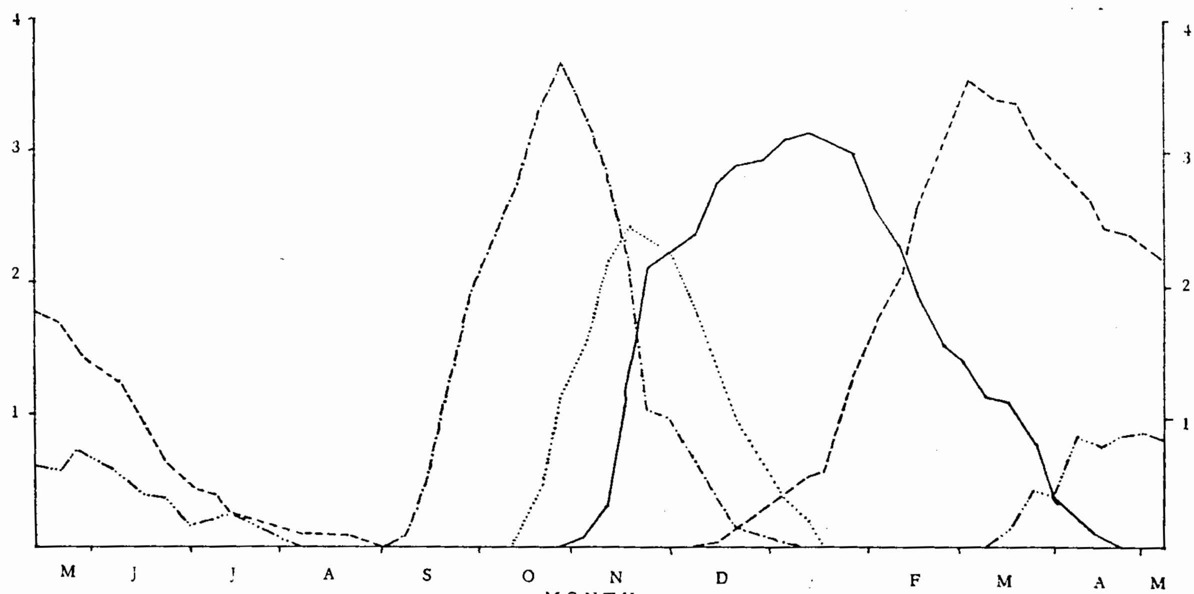


Figure 5. Reproductive phenology of Tapinanthus natalitius in the Loskop Dam Nature Reserve during 14 May 1977 - 6 May 1978. Phenological stages and y-axis as in Figure 4

quoted by Sprague 1925). I found only one possible case of host mimicry, namely between the leaves of T. leendertziae and those of Euclea crispa. Because T. leendertziae is quite unspecific with regard to hosts, however, this should rather be regarded as fortuitous.

4.1.3 Reproductive phenology of mistletoes

4.1.3.1 Annual cycles

Ninety-one individually-marked mistletoe plants were examined at weekly intervals during May 1977 - April 1978. During the course of the year seven of these plants died and another 11 lost their hosts (through death or breakage of branches of host trees). Twelve plants in the A. caffra - C. apiculatum community were inaccessible from September 1977 onwards, because of road building activities. Based on the marked plants surveyed (Table 4), the flowering and fruiting phenologies of the three common mistletoe species in the study area are shown in Figures 4 - 6.

In the two deciduous Tapinanthus species, both producing flowers and fruit seasonally, the first flower buds of T. natalitius appeared two weeks earlier than in T. leendertziae. Subsequent development differed markedly between the two species. The different phenological stages tended to be separate in T. natalitius (Figure 5), whereas in T. leendertziae the corresponding stages overlapped to a large extent (Figure 4). In the latter species, in some individuals young flower buds and ripe fruit occurred simultaneously, which was never the case in T. natalitius. The reproductive cycle of T. natalitius extended over the whole year, the first flower buds appearing two weeks after the ripe fruit disappeared. In contrast, the cycle of T. leendertziae lasted only 31 weeks.

The development of the first stage (immature flowers) was rapid in T. natalitius, reaching a peak after eight weeks, while in T. leendertziae the peak was reached after 16 weeks. Young flower buds of T. natalitius were produced only during the first part of the flowering period, whereas in T. leendertziae they were observed even at the end of the flowering period. The second stage (mature, open flowers) followed a similar pattern. If we consider the second stage as a direct indication

Table 4. The numbers of plants of three species of mistletoes, occurring in seven plant communities at the Loskop Dam Nature Reserve, which were surveyed for the incidence of flowers and fruit during May 1977 - April 1978. The first figures in each column indicate the number of plants at the start of the survey. The figures in brackets indicate the number of plants at the end of the survey

Name of plant community	Mistletoe species			
	T. leendertziae	*T. natalitius*	*V. combreticola*	
			Male	Female
Camp	4(3)	5(4)	0(0)	4(2)
A. caffra - *C. apiculatum*	4(3)	5(5)	1(1)	3(3)
A. caffra	4(4)	4(3)	1(1)	2(2)
A. karroo	8(7)	10(8)	2(2)	1(1)
C. apiculatum	3(2)	3(2)	3(3)	3(2)
Burkea	4(0)	1(1)	1(0)	3(2)
A. caffra - *F. saligna*	4(0)	4(0)	1(0)	3(0)
Total	31(19)	32(23)	9(7)	19(12)

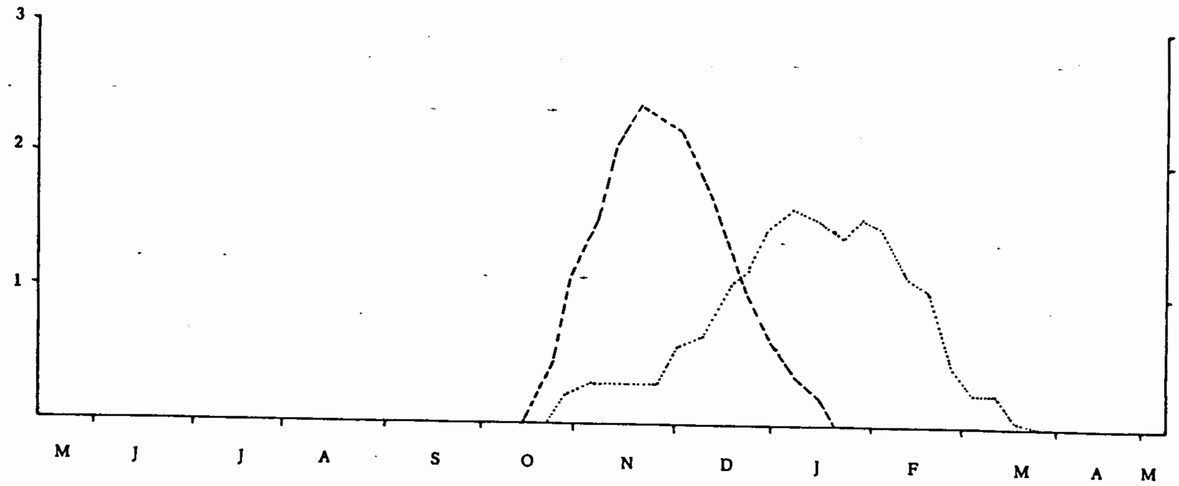


Figure 7. Relative nectar availability in T. leendertziae (··············) and T. natalitius (– – – – –) in the Loskop Dam Nature Reserve during 14 May 1977 - 6 May 1978. Y-axis as in Figure 4

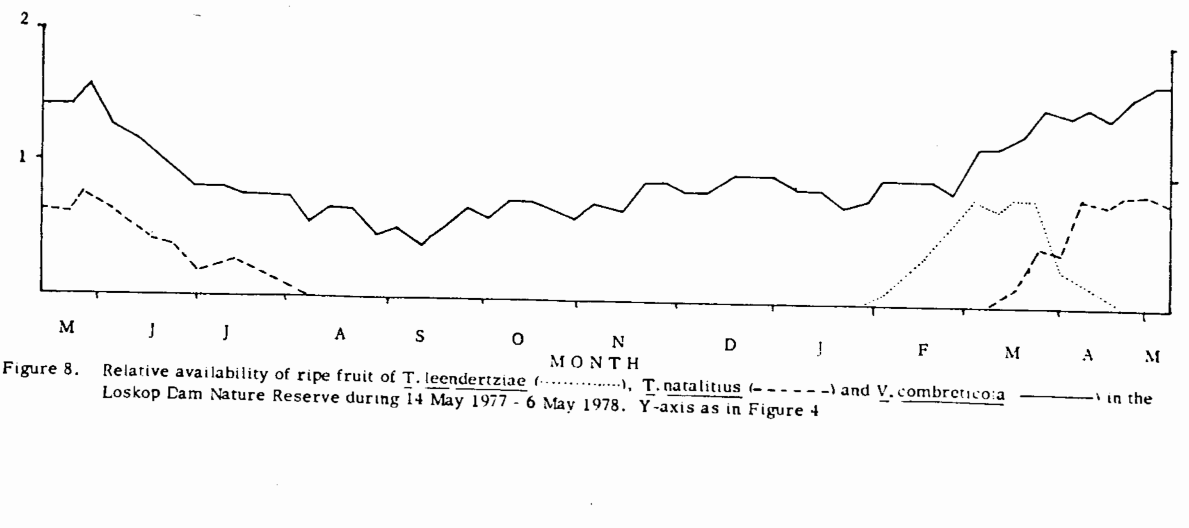


Figure 8. Relative availability of ripe fruit of T. leendertziae (··············), T. natalitius (– – – – – –) and V. combreticola (————) in the Loskop Dam Nature Reserve during 14 May 1977 - 6 May 1978. Y-axis as in Figure 4

of nectar availability, sunbirds were able to use Tapinanthus nectar for a period of 22 weeks. The open-flower stages of T. leendertziae and T. natalitius overlapped nearly completely, but the peaks differed; that of T. natalitius occurring seven weeks earlier than that of T. leendertziae (Figure 7). Tapinanthus natalitius flowers predominated during October - December, whereas T. leendertziae flowers were most abundant from January onwards. This separation of flowering peaks presumably results in a lowering of competition for pollinating agents between the two species. The development of fruit was much slower in T. natalitius than in T. leendertziae, which started producing ripe fruit six weeks earlier than T. natalitius.

A very poor crop of T. leendertziae fruit was produced during the 1978 season, probably mainly caused by storms during January and February, blowing off or damaging a large number of flowers and young fruit. In the previous season, during February and March 1977, a much more abundant crop had been produced, and although all T. leendertziae plants were covered by a mass of ripe fruit, the period of fruit abailability was the same as in 1978. It is likely that fruit production in T. leendertziae is at least three times higher in "good" years than in "poor" ones.

Because of the rapid development of fruit in T. leendertziae, a large crop is available during a relatively short period. The period of fruit abailability was 11 weeks for T. leendertziae, compared with 20 weeks for T. natalitius. The slow development of fruit in T. natalitius results in a low number of ripe fruit being available on a plant at any one time, with ripe fruit being produced for a relatively long period. During February and March T. leendertziae fruit was predominant, whereas T. natalitius fruit took over from April onwards, and the total period of availability of fruit of Tapinanthus species lasted 26 weeks (Figure 8). The separation of fruiting periods results in lower competition for dispersal agents. The large fruit crop made available by T. leendertziae plants, attracted a relatively wide variety of dispersal agents (Table 10). Because of the low number of fruit of T. natalitius available at any one time, they are removed mainly by the "mistletoe-specialist" Yellowfronted Tinker Barbet which apparently recognizes ripe fruit when they are in an early stage of maturation (see Section 4.2.3.2).

The start of the reproductive cycles in both Tapinanthus species is possibly inter alia triggered by their hosts becoming physiologically more active after the "winter rest".

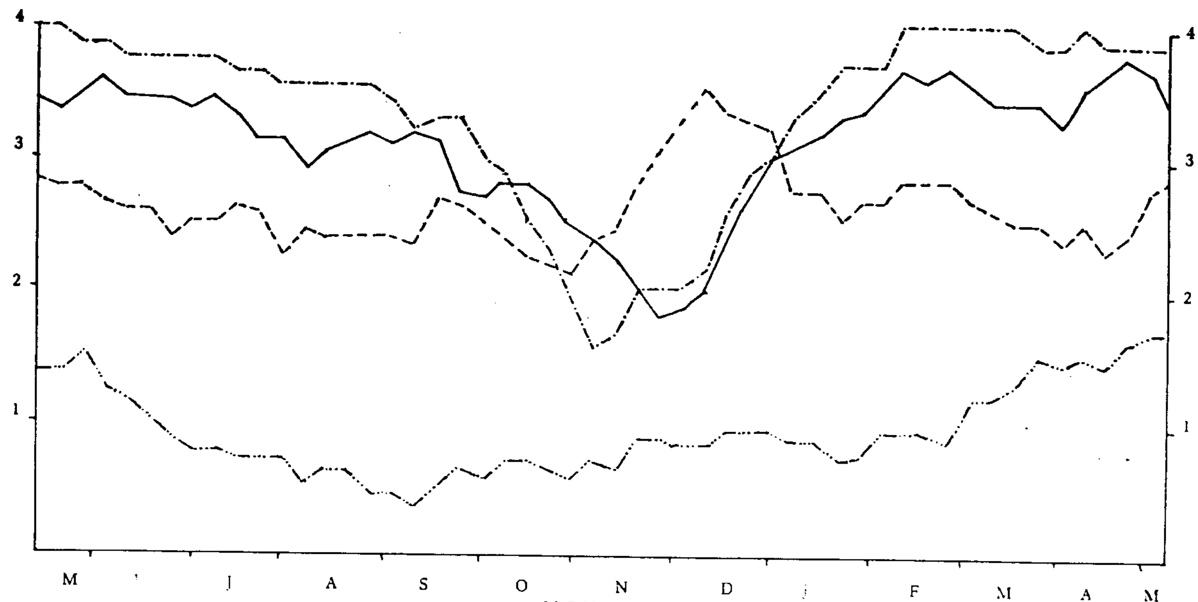


Figure 6. Reproductive phenology of Viscum combreticola in the Loskop Dam Nature Reserve during 14 May 1977 - 6 May 1978. Different phenological stages: male flowers (—·—·—), female flowers to very young fruit (———), unripe fruit (– – – –), ripe fruit (—·····—). Y-axis as in Figure 4

Their main host in the study area was Acacia caffra which was deciduous. Tapinanthus n atalitius rapidly produces many flowers. Perhaps because of this large energy investment, development is slow after pollination. This applies especially to the later stages of fruit development, resulting in a slow rate of fruit maturation. In T. leendertziae, on the other hand, the production of flowers is relatively slow, and it is possible that energy is conserved for utilization during the rapid mass production of fruit. Although the exact physiological basis for this difference in reproductive cycles between T. leendertziae and T. natalitius is not known, it apparently results in an effective decrease in competition for pollinating and dispersal agents. It is remarkable that, while the timing of the start of the cycles in both species is nearly the same, T. natalitius produced flowers earlier, but fruit later, than T. leendertziae.

The reproductive strategy of Viscum combreticola is completely different (Figure 6). Because the stems perform the photosynthetic function, it is an evergreen plant producing food continuously. Consequently, flowers and fruit can be produced continuously, as was observed during this study. Although the Combretum species (the main hosts of V. combreticola) produce young leaves in spring, they were observed to have leaves throughout the winter, probably indicating a certain amount of physiological activity. This may also have assisted V. combreticola in producing flowers and fruit throughout the winter. Because V. combreticola is a dioecious mistletoe (Sprague 1925), the results for male and female plants are given separately (male plants were considered to be those which did not produce any fruit during the year-long survey). The flowering phenologies of male and female plants were similar (Figure 6). Whether the depressed incidence of flowers during October - December has any functional correlation with the occurrence of hymenopterids (presumably the main pollinators, see Section 4.1.1), or whether it has to do with climatic conditions, is not known. More rapid formation of unripe fruit during this period (see Figure 6) may also decrease the number of very young fruit (included in the first stage) in female plants. Because fruit is produced continuously, mass crop production is probably not possible and relatively low numbers of ripe fruit are available on a plant at any one time (but more than in T. natalitius). Consequently, generalist fruit-eating birds are not attracted in large numbers and the "mistletoe specialist" Yellowfronted Tinker Barbet consumes 94% of the fruit of V. combreticola (Table 10).

During July - February the number of available ripe fruit of V. combreticola was lower than during March - June (Figure 8). During the former period fruit of both Tapinanthus species was absent (except for small numbers in July and February). Unripe fruit of V. combreticola, however, was present in large numbers during that period. This indicates that in the absence of other mistletoe fruit, the feeding pressure on V. combreticola fruit is so high (the high rate of removal of V. combreticola fruit during this period (Figure 10, Section 4.2.2) supports this suggestion) that the number of ripe fruit is kept constantly low. When Tapinanthus fruit become available, the birds partly switch to these fruit and therefore the feeding pressure on V. combreticola fruit is reduced to a certain degree (see Figure 10), resulting in more ripe fruit available on the plants. The same phenomenon (a reversed relationship between number of ripe fruit available and feeding pressure) was also found for the mistletoe Oryctanthus occidentalis in Panama (Leck 1972) and Loranthus longiflorus in India (Ali 1931).

As far as I am aware, only two studies of the flowering and fruiting phenologies of African mistletoes have been published. Liversidge (1972) studied the fruiting phenologies of a number of fruit-bearing plants near Port Elizabeth, including the Cape mistletoe Viscum capense. According to Liversidge's text, fruiting in V. capense occurred in spring and autumn, but his Figure 2 shows that fruit was available at any time of the year though not continuously. Room (1973) found two flowering and two fruiting peaks in a year in T. bangwensis growing on cocoa trees in Ghana, and Frost (pers. comm.) found the same condition in Erianthemum dregei in Natal. These two mistletoe species both were growing predominantly in forest habitat. Short flowering and fruiting periods (one to two months) were observed by Frost (pers. comm.) for V. capense in coastal fynbos vegetation in the Cape, and also for V. rotundifolium in secondary forest near Kirstenbosch in the Cape. Much more information is needed on the flowering and fruiting phenologies of more species of mistletoes at a variety of localities and in different habitats and climatic regimes, and extended over a period of at least one year (but preferably longer), to get a general picture of the factors influencing the production of flowers and fruit. It is important, however, that further studies should pay attention not only to presence or absence of flowers and fruit, but also to the relative abundance of flowers and fruit (as in this study). It is important that any differences in peak-times of flowers and fruit should be revealed, as indicated above (Figure 7).

Some data on the flowering and fruiting of Erianthemum ngamicum and V. rotundifolium are given in Appendix 2.

4.1.3.2 Individual plants

Table 5 shows the duration of different reproductive stages in individual plants of T. leendertziae and T. natalitius. The periods between the first appearances of the different stages can be considered to be rough indicators of the development of individual flowers. Seventeen weeks were required for the development of flower buds to mature fruit in T. leendertziae, compared with 28 weeks in T. natalitius. The main difference rests in the slower development of fruit in T. natalitius. A fruit required seven weeks for complete development in T. leendertziae; it required 20 weeks in T. natalitius. The flower stages are crammed into a relatively short period (22 weeks) in T. natalitius. The corresponding stages lasted 30 weeks in T. leendertziae. If equal numbers of flowers are to be produced in both species (a subject for which no data are available), then T. natalitius would use energy for flower production at a faster rate than T. leendertziae, which may be related to the former species' relatively slow development of fruit. However, other factors, like climatic conditions (different months in which ripening takes place) and fruit quality, may also be involved (the fruit of T. natalitius is, indeed, somewhat larger than that of T. leendertziae).

The mean duration of the reproductive cycle for individual plants of T. leendertziae was 22 weeks (Table 5), or 71% of the duration (31 weeks) of the cycle in the whole population (Figure 4). In the case of T. natalitius the mean individual plant's cycle amounted to 40 weeks which is 78% of the duration of the cycle (51 weeks) in the population (Figure 5). In effect, this means that the reproductive stages of T. natalitius plants were more closely synchronized than in T. leendertziae.

Most individual male plants of V. combreticola bore flowers (stage 1) throughout the year. Some of these plants produced a seemingly equal abundance of flowers throughout the year, but in others a marked decline in the number of flowers was observed during October - December. Female plants had flowers and unripe fruit (stage 1) throughout the year, but the production of flowers declined in most plants during October - December; the quantity of unripe fruit increased during November - December. Ripe fruit was present for periods of 7 - 49 weeks on individual plants, with lower numbers during June - February.

Table 5. Mean duration (number of weeks) of reproductive stages for individually-marked plants of Tapinanthus leendertziae (18 plants in sample) and T. natalitius (23 plants in sample)

Phenological stages	T. leendertziae $\bar{x} \pm$ S.D. (range)	T. natalitius $\bar{x} \pm$ S.D. (range)
Flowerbuds - closed flowers	17±2,7 (13 - 22)	12±1,6 (9 - 17)
Open flowers	13±3,6 (6 - 17)	10±1,9 (6 - 13)
Very young fruit	10±2,8 (5 - 15)	19±2,8 (13 - 24)
Unripe fruit	6±1,7 (3 - 9)	22±5,9 (12 - 37)
Ripe fruit	4±2,8 (0 - 9)	8±5,4 (0 - 19)
First flowerbud - first open flower	5±2,1 (1 - 10)	5±0,9 (4 - 7)
First open flower - first very young fruit	5±2,8 (1 - 12)	3±1,0 (0 - 5)
First very young fruit - first unripe fruit	5±2,3 (0 - 9)	9±2,1 (5 - 12)
First unripe fruit - first unripe fruit	2±0,9 (1 - 4)	11±3,1 (6 - 17)
Whole cycle	22±2,9 (17 - 27)	40±5,4 (30 - 51)

4.1.4 Pollination of mistletoes

Nectar is produced at the bottom of the corolla tube in mature Tapinanthus flowers. The stigma, surrounded by the anthers just below it, occupies the uppermost part of the flower-head (illustrated in Room 1973).

When flowers of T. natalitius are mature, short subapical slits are formed between the petals on the throat and lower part of the head of the flower (illustrated in Pole-Evans 1937). A visiting sunbird (Family Nectariniidae) inserts its beak into one of the slits and, by moving its beak downwards, "unzips" the corolla tube unilaterally. When the beak is halfway down the tube, the pressure on the still-connected petal tips becomes too great and the tips separate but stay erect (illustrated in Pole-Evans 1937). At this moment the pressure which kept the stamens in the head, is released, and the stamens curl in- and downwards suddenly, throwing the pollen on the bird's head. Simultaneously, the style bends to one side at an angle of approximately 40°, in which position it is easily touched by the head of the next avian visitor, thus receiving pollen. This process of flower-opening seems to be basically similar to that found in some other mistletoes, such as Phragmanthera dshallensis (Gill & Wolf 1975), T. kraussianus and Erianthemum dregei, though in the latter even the anthers themselves are dehisced during the explosive curling of the stamens (Evans 1895). Evans found that no pollen was thrown into the stigma during this process, presumably to prevent self-pollination. He also suggested that the flowers of E. dregei are protandrous (i.e., the stigma maturates after the pollen has been released) to prevent self-pollination, since he found stigmas in mature flowers to be dry, whereas receptive stigmas were rather sticky to facilitate retention of pollen deposits. If this is so, nectar should be produced after flower-opening, too, to attract birds subsequently in affecting pollination. Gill and Wolf (1975) found that nectar was indeed produced in flowers of P. dshallensis for about 2-3 days after flower-opening, but in smaller amounts than just before opening, and that sunbirds did feed on already opened flowers.

Orange-fruit bags were placed over two branches of the same T. natalitius plant; each branch bearing 21 and 28 unopened, nearly mature flowers, respectively. The mesh-size of the bags was large enough to allow insects to pass through. Almost the normal amount of sunlight reached the branches, so that physiological processes were not hampered. The "bagged " flowers reached the stage of slit-formation, but none was opened further. Consequently, no fruit was formed. On neighbouring branches of the same plant fair numbers of fruits were formed. Evans (1895) found that "bagged" flower-bearing branches of T. kraussianus did not produce fruit. This type of flower-opening makes the plant apparently entirely dependent on birds for pollination. In P. dshallensis, however, a few flowers did open spontaneously (Gill & Wolf 1975). It is remarkable that the process of flower-opening in T. kraussianus and T. natalitius seems to be similar to that in E. dregei and P. dshallensis, while it differs from the process in their congenerics T. leendertziae and T. bangwensis as discribed below.

When flowers of T. leendertziae become mature, the margins between the petals on the flower-head become dark which can be regarded as a signal to birds, indicating maturity of the flower and thus availability of nectar. The visiting sunbird squeezes the flower-head with its beak. This causes the petal tips to separate and to reflex out- and downward, exposing the stigma surrounded by the anthers just below it (stage 1). Then the bird inserts its beak between the style and the corolla, and, moving it down, unzips the corolla tube unilaterally (stage 2). The pressure of the tube which kept the stamens together, falls away and they curl downwards explosively, releasing the pollen onto the bird's head, and simultaneously the style bends to one side, as in T. natalitius. The flower-opening process in T. leendertziae seems to be similar to that reported for T. bangwensis by Room (1973) who clearly illustrated the two stages (head-opening and corolla-splitting) in the process. I observed the first stage several times in T. leendertziae and it appeared that this stage could be initiated also by internal pressure alone , as recorded for T. bangwensis (Room 1973), because it is improbable that a sunbird would open the flower-head without opening the corolla tube to obtain nectar.

Three branches of different T. leendertziae plants bearing together at least 100 flowers, were "bagged" in the same way as in T. natalitius. More flowers were probably formed during the experiment, because of the continuous formation of flowers in this species (see Section 4.1.3.1). The flower-heads remained either closed or did open, but no corolla tubes were split. Three fruit were formed eventually on the "bagged" branches in contrast to the large number of fruit formed on "unbagged" branches of the same plants. The formation of three fruit on "bagged" branches indicates that limited pollination can take place even without birds, probably by insects. Since the stigma and the anther are exposed when the flower-head opens, it seems likely that some pollen may be carried from the anthers to the stigma by insects walking over the flowers.

Ants were present on Tapinanthus plants in large numbers, continuously walking over the branches, flowers and fruit, and possibly were the agents for pollination in the few cases where fruit were formed. Thus, although pollination can take place in T. leendertziae without the aid of birds, this is undoubtedly too small to make the species independent of bird pollination.

Tapinanthus natalitius appears to be entirely, and T. leendertziae mostly dependent on sunbirds for pollination. The distribution of Tapinanthus species (and probably of all loranthoid species, Kuyt 1969) is therefore not only affected by the presence of birds as dispersors of seeds but also by the presence of birds for pollinating the flowers. In the study area, the Whitebellied Sunbird Nectarinia talatala and the Black Sunbird N. amethystina were observed to feed regularly on the nectar of both Tapinanthus species.

The Masked Weaver was observed to prey on the flowers of T. leendertziae in two ways. Firstly, it was observed to bite off and to swallow the flower-heads, presumably for the pollen. Such decapitated flowers were encountered regularly in the field. Secondly, the bird was observed to pluck whole flowers and to squeeze their bases, apparently to obtain nectar.

4.1.5 Germination of mistletoes

After the seeds have been deposited on a host branch, the viscin of Viscum seeds dries rather quickly to cement the seed firmly to the branch. The viscin of Tapinanthus seeds remains softer (pers. obs.), possibly because it may hold water to aid in germination (see Section 4.1.1). Tapinanthus seeds germinated within a week, whereas germination took longer in Viscum (pers. obs.). The hypocotyl of Tapinanthus invariably broke through the viscin at the distal (broad) end of the seed. The hypocotyls can appear at any part of the rounded seed of V. rotundifolium. In the flattened V. combreticola seeds, however, the hypocotyls tended to appear on the margins.

The physical factors influencing germination of mistletoe seeds are discussed extensively by Gill and Hawksworth (1961). Mistletoe hypocotyls are apparently negatively phototropic, thus growing in the direction of the darkish host branch. Mistletoes are light-loving plants (see Room (1973) for quantitative data for T. bangwensis) and seeds

Table 6. Germination of mistletoe seeds after various types of treatment

Type of seed treatment	*T. natalitius* ssp. *zeyheri*		*V. rotundifolium*	
	No. seeds planted	No. seeds germinated	No. seeds planted	No. seeds germinated
Defaecated by Crested Barbet	3	2	25	22
Regurgitated by Crested Barbet	11	9		
Defaecated by Blackeyed Bulbul			50	46
Defaecated by Cape White-eye			1	1
Defaecated by Kurrichane Thrush			6	5
"De-exocarped" seeds	15	13	25	21

Using Fisher's exact method for 2x2 tables (for procedure see Ostle 1963), germination of seeds was not influenced significantly ($P \leq 0,05$; the lowest P-value found was 0,24) by passage through the alimentary tract of a bird.

germinate relatively weakly in shade.

A much debated question is whether the passage of a seed through a bird's alimentary tract is essential for its germination. Evidence against the essential role of a bird depends on the fact that germinating seeds are found occasionally in unopened, very ripe fruit (Marloth 1913; Batten & Bokelmann 1966; pers. obs.). In order to experimentally investigate the controversy, I planted seeds of T. natalius ssp. zeyheri and V. rotundifolium, defaecated or regurgitated by four species of birds, on a Combretum erythrophyllum tree. I also planted seeds from which I had removed the exocarp and the aril, as control groups (Godschalk 1976). The results of the tests are shown in Table 6, pointing to the conclusion that passage through the alimentary tract of a bird does not improve a seed's germination. Birds are, however, apparently required to remove the exocarp and the aril (which is the actual bird attractant) to facilitate contact between the viscin and the host branch. Schönland's (1913) suggestion that seed dispersal in Erianthemum dregei is not by means of birds, but that the fruit simply falls onto a branch, splits and adheres by means of the exposed viscin, is far-fetched and was not based on actual observation. Moreover, the condition he found, described, illustrated, and on which he based his suggestion, is exactly what is found when the seeds are deposited by birds.

4.1.6 Biochemical composition of the fruit of Tapinanthus leendertziae

Data on the biochemical composition of the various components of T. leendertziae fruit are given in Table 7. The ash and energy values for the aril were derived indirectly from directly determined values for seeds and arillate seeds. The differences between directly and indirectly obtained values for the aril in the case of the protein, lipid and crude-fibre-and-ash determination (which could be checked), were only 1, 4 and 7%, respectively, which suggests that the indirect derivations, and reasonably reliable. The energy content could also be calculated indirectly by summing the energy contents of the different fractions using 5, 65 cal/mg for protein, 9, 45 cal/mg for lipids and 4, 10 cal/mg for carbohydrates (including the NF E and crude fibre) as conversion factors (Paine 1971). This indirect energy estimation resulted in 6 092 and 6 388 cal/g for the aril and the seed, respectively, which differs by 0, 9 and 5, 2%, respectively, from the values obtained by means of a microbomb calorimeter. The red pigment in the aril is soluble in petroleum ether, being completely removed by

Table 7. Biochemical composition of various parts of the fruit of Tapinanthus leendertziae

Values expressed as percentages per gram dry weight unless otherwise indicated; "ind." indicates that the value was derived indirectly (see text for explanation); NFE is explained in Section 3.2; the figures in parentheses indicate the number of replicate determinations (see Section 3.2 for sampling procedure).

	Seed $\bar{x} \pm$ S.D.	Aril $\bar{x} \pm$ S.D.	Exocarp $\bar{x} \pm$ S.D.
Fresh weight (mg)	179,6 ± 8,00 (4)	78,7 ± 8,61 (4)	190,4 ± 13,26 (7)
% water (fresh)	51,5 ± 0,90 (3)	75,2 ± 1,20 (3)	77,1 ± 0,82 (7)
Energy (cal/g)	6 071 ± 172 (5)	6 148 (ind.)	
Protein	6,9 ± 0,22 (3)	9,1 ± 0,21 (2)	
Lipids	41,3 ± 1,06 (4)	34,7 ± 0,54 (2)	
NFE	50, 2 (ind.)	47,9 (ind.)	
Crude fibre	0,9 (ind.)	7,7 (ind.)	
Ash	0,7 ± 0,84 (3)	0,6 (ind.)	

Soxhlett-extraction. The finely-ground material of the seeds and arillate seeds was extremely sticky and difficult to handle, because of the viscin. The viscin was apparently dissolved or neutralized, leaving behind a non-sticky powdery residue, during the petroleum-ether extraction process.

The data in Table 7 are apparently the first for any African mistletoe. They are apparently also the first for an analysis in which the attractant for the dispersor (the aril) of mistletoe fruit has been treated separately. The protein content of the aril is higher than in the seed, but the lipid content lower. The latter is probably important as a food supply for the embryo in the seed. The reason for the high fibre content of the aril is not clear. The energy values of the aril and the seed are nearly identical. Included in the seed is, of course, also the viscinlayer which seems to consist mainly of pectose in Loranthus europaeus and of pectose and cellulose in Viscum album (Tomann 1906; Schiller 1928; Mangenot et al. 1948). In the case of T. leendertziae 29% of the dry weight is invested in the exocarp for protection during maturation; 13% in the aril for attraction of dispersal agents and 58% in the seed, partly for attachment and partly for the actual next generation. The contribution of the seed and aril was only 34% of the fresh weight of 13,2 g of fruit (n = 100) of V. combreticola.

From older reports in the literature it is not always clear which fractions are comparable to those obtained in more recent analyses, because the methods were not standard. Hence, care is needed in comparing old and modern results. Schiller (1928) found lipids to comprise 36% (dry weight) of whole Loranthus europaeus fruit, which is similar to what I found in T. leendertziae. Walsberg (1975b) found 15% lipids and 1,2% nitrogen (= 7,5% protein), on a dry weight basis, in whole fruit of Phoradendron californicum (a viscoid species). The energy content was 5 280 cal/g dry weight (which was 15,9 mg/fruit). Crome (in appendices to his 1975 paper) reports 81,5% water content, 8,29% protein and 4,5% lipids, on a dry weight basis, in the "flesh" (i.e., seed and aril) of fruit of Notothixos subaureus (a viscoid species). The fresh weight of the fruit was 110 mg of which the "flesh" made up 96,7%, a condition similar to that found in a number of South African Viscum species (e.g. V. capense and V. rotundifolium which have very thin exocarps, too). The reported protein values for P. californicum and N. subaureus are similar to those in T. leendertziae, but the lipid contents of the former two species are considerably lower. The energy content of P. californicum fruit was much lower than in the aril or the seed of T. leendertziae, which can be attributed to the relatively low lipid content of the former species. Because no previous analyses of arils have been carried out, it is difficult to make general comparisons. The reported lower lipid values for two viscoid species and the higher values in two loranthoid species may, however, indicate differences in the nature of the arils between the two subfamilies. The arils of V. combreticola and other Viscum species are composed of a jelly-like substance and presumably have a lower lipid content than those of loranthoids.

The proportion of different amino acids in the protein fraction of the aril of T. leendertziae fruit is shown in Table 8. Aspartic acid is the most important amino acid, constituting 20%. To my knowledge, the only other detailed analysis of amino acids of mistletoe fruit was carried out by Chiarlo and Cajelli (1965) on whole fruit of Loranthus europaeus. Again, care should be taken in making comparisons, as different types of material (arils and whole fruit) were analyzed, but it appears that L. europaeus fruit has high proline and low leucine and valine contents in comparison with T. leendertziae (Table 8).

Although the aril of T. leendertziae fruit contains 75% water, the high lipid and protein contents place it in the category of fruits taken by "specialized" fruit-eating birds (Snow 1962, 1971). "Generalized", succulent fruits provide mainly water and carbohydrates to a wide variety of birds, whereas fruits taken by a few "specialized" fruit-eaters provide mainly lipids and protein, which are the main source of energy and nitrogen building material for these birds (Snow 1971; McKey 1975). The implications of this are discussed in Section 5.2.1.

Using King's (1974) tentative equation for total daily energy expenditure (DEE) in free-living birds, we can roughly estimate the number of fruits of T. leendertziae needed in providing the energy requirements of the Yellowfronted Tinker Barbet. King's equation reads: $DEE = 317,7 + W^{0,7052}$, where DEE is in kcal/day and W is body weight in kilograms. With W specified as 0,0125 kg, the estimation of DEE is 14,45 kcal (60,208 kJ) per bird per day, which means that 120,4 T. leendertziae fruits are needed to satisfy the bird's energy requirements, at 100% efficiency. If we assume a digestive efficiency of 70% (which seems reasonable, since Walsberg

Table 8. A comparison of the amino acid composition of the protein fractions of the aril of fruit of Tapinanthus leendertziae and of whole fruit of Loranthus europaeus (data for the latter species obtained from Chiarlo and Cajelli 1965). Values expressed as percentages of total protein fractions, on a dry weight basis

Amino acids	T. leendertziae aril	L. europaeus fruit
Aspartic acid	19,6	16,5
Arginine	9,7	8,4
Glutamic acid	9,7	7,0
Proline	9,7	45,0
Leucine	7,6	<1
Alanine	5,6	4,1
Serine	5,4	2,15
Valine	5,4	<1
Lysine	4,8	9,2
Glycine	4,4	1,43
Threonine	4,4	<1
Isoleucin	4,2	<1
Phenylalanine	4,1	<1
Histidine	2,8	-
Tyrosine	2,6	1,01
Cysteine	-	2,1
Methionine	-	<1

(1975b) found 49% caloric utilization efficiency in Phainopepla nitens feeding on mistletoe fruit, but he took into account the whole fruit, whereas the seed is not digested at all), 172 fruits per bird per day are needed. In this calculation it was assumed that the bird takes only mistletoe fruit for its energy requirements, whereas, in fact, insects are taken too (see Section 4.2.6). The actual number of fruits consumed may thus be lower. Unfortunately, however, no data on the actual intake of fruit per day are available. The arils of 172 fruits of T. leendertziae contain 10,2 g water (81% of the bird's body weight), which is more than enough for the bird's water requirements.

4.2 Ornithological aspects

4.2.1 Fruit- and mistletoe-eating birds

Included under fruit-eating birds are all species recorded by McLachlan and Liversidge (1978) as taking berries and other fruit, and birds of all species observed by me to eat fruit in the study area (the following species are additional to those in McLachlan and Liversidge (1978): Arrowmarked Babbler, Kurrichane Thrush, Redheaded Weaver, Spottedbacked Weaver, and Yelloweye Canary); and, the Cape Weaver, because according to Rowan (1970) most Ploceus species, included the Cape Weaver (see also Elliott 1973), include fruit in their diet. Twenty-seven species of fruit-eating birds were recorded within 40 m of mistletoe plants (Table 9). Eight species were observed to eat mistletoe fruit (Table 10).

The Yellowfronted Tinker Barbet was by far the most important eater of mistletoe fruit in the reserve throughout the year (Tables 10-12). This finding tends to confirm the general statements in the literature as to the preference of this species for mistletoe fruit (see Section 2). Apart from the numerous records of feeding on the fruits of the three common mistletoe species, the Yellowfronted Tinker Barbet was observed once to eat V. rotundifolium fruit and it was the only species observed to eat E. ngamicum fruit on a few occasions. This bird was almost never seen close to a mistletoe plant without feeding on its fruit.

The widespread Redfaced Mousebird, eating fruit of T. leendertziae and V. combreticola, was of importance only in the A. caffra - F. saligna community (Table 11). It was also

Table 9 Fruit-eating birds observed within 40 m of mistletoe plants in different plant communities in the Loskop Dam Nature Reserve. X indicates presence of bird

Bird species	Abundance	Plant communities						
		1	2	3	4	5	6	7
Redeyed Turtle Dove *Streptopelia semitorquata*	L	X	X				X	X
Green Pigeon *Treron australis*	M	X						
Grey Loerie *Crinifer concolor*	L	X	X	X	X		X	X
Speckled Mousebird *Colius striatus*	H	X			X			X
Redfaced Mousebird *C. indicus*	H	X	X	X	X		X	X
Grey Hornbill *Tockus nasutus*	L	X	X	X	X	X	X	X
Yellowbilled Hornbill *T. flavirostris*	L		X	X	X	X		
Blackcollared Barbet *Lybius torquatus*	L	X		X	X		X	X
Pied Barbet *L. leucomelas*	L		X		X			
Yellowfronted Tinker Barbet *Pogoniulus chrysoconus*	L	X	X	X	X	X	X	X
Crested Barbet *Trachyphonus vaillantii*	L	X	X	X	X	X	X	X
Black Cuckooshrike *Campephaga phoenicea*	L			X	X	X		X
Blackheaded Oriole *Oriolus larvatus*	L	X	X	X	X	X	X	X
Southern Black Tit *Parus niger*	M	X	X	X	X	X	X	X
Arrowmarked Babbler *Turdoides jardineii*	M	X	X	X	X	X		X
Blackeyed Bulbul *Pycnonotus barbatus*	MH	X	X	X	X	X	X	X
Kurrichane Thrush *Turdus libonyana*	L	X	X		X			X
Cape Robin *Cossypha caffra*	L	X						
Titbabbler *Parisoma subcaeruleum*	L		X		X			
Plumcoloured Starling (S) *Cinnyricinclus leucogaster*	MH	X	X		X			X
Cape Glossy Starling *Lamprotornis nitens*	MH	X	X	X	X		X	X
Redwinged Starling *Onychognathus morio*	MH	X	X		X			X
Cape White-eye *Zosterops pallidus*	M	X	X	X	X	X	X	X
Redheaded Weaver (?S) *Anaplectes rubriceps*	M			X	X			
Cape Weaver *Ploceus capensis*	L	X	X					
Masked Weaver *P. velatus*	MH	X	X					X
Yelloweyed Canary *Serinus mozambicus*	L	X	X	X	X		X	
Total no. of species 27		22	21	15	22	10	13	19

S = A summer migrant

The letters L (= 1-2 birds), M (= 3-6 birds) and H (7 or more birds) indicate the size of flocks normally observed near mistletoe plants

Plant communities: 1 = camp, 2 = *A. caffra* - *C. apiculatum*, 3 = *A. caffra*, 4 = *A. karroo*, 5 = *C. apiculatum*, 6 = *Burkea*, 7 = *A. caffra* - *F. saligna*.

Table 10. Relative frequency of records of birds feeding on fruit of mistletoes in the Loskop Dam Nature Reserve during March 1977 - April 1978. All figures are percentages

	Mistletoe species		
Bird species	T. leendertziae	T. natalitius	V. combreticola
Speckled Mousebird (os)			
Redfaced Mousebird	6		2
Blackcollared Barbet	4	5	2
Pied Barbet	5	6	1
Yellowfronted Tinker Barbet	64	80	94
Southern Black Tit	8	9	0,2
Plumcoloured Starling	9	or	
Redheaded Weaver	3		
No. records	409	85	665

os = recorded to eat fruit of other mistletoes in the area
or = recorded outside observation periods

Table 11. Relative frequency of records of bird species feeding on fruit of mistletoes (*T. leendertziae*, *T. natalitius*, and *V. combreticola*) in seven communites of plants in the Loskop Dam Nature Reserve during March 1977 - April 1978. All figures are percentages

	Plant communities						
Bird species	Camp	*A. caffra* - *C. apiculatum*	*A. caffra*	*A. karroo*	*C. apiculatum*	*Burkea*	*A. caffra* - *F. saligna*
Redfaced Mousebird	3	or	7	P		P	37
Blackcollared Barbet	3		4	8		12	P
Pied Barbet		10		1			
Yellowfronted Tinker Barbet	92	69	82	90	98	88	56
Southern Black Tit	P	11	P	1	2	P	5
Plumcoloured Starling	3	10		P			2
Redheaded Weaver			7	P			
No. records	162	305	208	117	180	130	57

or = recorded outside observation periods
P = present but not recorded eating mistletoe fruit

Table 12. The number of monthly records of birds feeding on fruit of mistletoes (<u>T. leendertziae</u>, <u>T. natalitius</u> and <u>V. combreticola</u>) in the Loskop Dam Nature Reserve during March 1977 - April 1978 (April 1977 excluded)

Bird species	March	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Redfaced Mousebird	21									14		5	
Blackcollared Barbet	8	4								7	2	8	8
Pied Barbet	15	3					4				7		2
Yellowfronted Tinker Barbet	142	21	25	66	122	125	69	21	60	54	86	103	65
Southern Black Tit	36				1						4		
Plumcoloured Starling	29	M	M	M	M	M					or	8	or
Redheaded Weaver	14	?M	?M	?M									

M = summer migrant not present in study area
or = recorded outside observation periods

seen several times in V.combreticola plants, together with Speckled Mousebirds, without eating fruit. The Re dfaced Mousebird has apparently not formerly been recorded as eating fruit of a loranthoid mistletoe.

The Blackcollared Barbet was observed to eat fruit of all three common mistletoe species (Table 10). In captivity, it ate V. rotundifolium fruit. The absence of this otherwise wide-spread bird from the A. caffra - C. apiculatum community (Table 9) was probably related to the openness of the vegetation, since the species prefers rather well-wooded habitat (Skead 1950). The species was of some importance (12%) only in the Burkea community (Table 11). The feeding records were distributed from January to May, i.e., late summer and autumn (Table 12). It is remarkable that Blackcollared Barbets were not seen feeding on V. combreticola fruit in the camp (see Appendix 3), because a pair occupied a hole in a Combretum zeyheri tree in the camp very close to a large V. combreticola which I had under regular observation. The birds were seen perched on top of the mistletoe plant, but did not make any attempt to feed on the ripe fruit available. The Blackcollared Barbet has been recorded to eat Viscum fruit (Anon. 1963c), but I could not find any published information for it feeding on loranthoid fruit.

The Pied Barbet was very uncommon in the study area. One bird was seen regularly in the A. caffra - C. apiculatum community (Table 11). Otherwise, the species was seen only once at the boundary of the reserve, and heard or seen a few times in the N.E.V. where the only record of mistletoe fruit-eating for this species outside the A. caffra - C. apiculatum community was obtained. It was recorded feeding on the fruits of all three common mistletoes. The Pied Barbet has been recorded as eating Loranthus fruit (Anon. 1962), but not Viscum fruit , as was found in this study.

The Southern Black Tit was recorded as eating the fruits of T. leendertziae, T. natalitius and V. combreticola, but mainly those of Tapinanthus (Table 10). It was of some importance (11%) in the A. caffra - C. apiculatum community (Table 11), though it occurred widespread throughout the reserve (Table 9). I could not find in the literature any record of the Southern Black Tit feeding on mistletoe fruit.

The Plumcoloured Starling was recorded as eating the fruits of T. leendertziae and T. natalitius, though the latter only once. All records were obtained during February

- April (Table 12), which is explained by the fact that T. leendertziae fruit becomes available during February and the birds emigrated in April. The bird was of some importance (10%) in the A. caffra - C. apiculatum community (Table 11). During March 1977, when a good crop of T. leendertziae fruit was available, the bird was observed to feed freely on the fruit of this mistletoe, in flocks of varying size. The Plumcoloured Starling may, therefore, be more important than emerges from Table 10. In March 1976 I saw it eating fruit of T. natalitius ssp. zeyheri near Pretoria (Godschalk 1976). It was seated close toa V. combreticola plant without showing any intention of feeding on the available ripe fruit. This is apparently the first record of the Plumcoloured Starling eating mistletoe fruit.

A flock of Speckled Mousebirds was once observed to eat many fruits of V. rotundifolium in the Camp. Though the birds visited T. leendertziae and V. combreticola plants with ripe fruit several times - even nesting in the former - they were not observed to eat the fruit. In fact, they actually ate the flowers of V. combreticola while disregarding the neighbouring ripe fruit.

The difference in the distribution of the birds and the feeding records between the plant communities will be discussed in Section 5.1. Tapinanthus leendertziae had the widest variety of potential avian dispersors (Table 10), which may partly be explained by the relatively high number of ripe fruit available on individual plants at one particular time (see Section 4.1.3.1). It should be borne in mind that the ripe fruit of T. leendertziae is bright red, compared with green, yellow and darkish red (the last stage is seldom seen) in T. natalitius and dull orangish-red in V. combreticola. Ripe T. leendertziae fruit, contrasting the most with the green background, are more conspicuous to man in the field than fruit of T. natalitius and V. combreticola (pers. obs.), and apparently the visual perception of birds is at least comparable to that of man, and for red, possibly even better (Faegri & Van der Pijl 1966; Raven 1972). Turček (1963) showed experimentally that red diaspores were preferred strongly by a wide variety of birds (156 species), and that fewer green and yellow diaspores were eaten than could be expected by chance. A limited colour-preference experiment that I carried out with a Crested Barbet, however, showed that the bird preferred green mistletoe fruit over red ones (see Appendix 5). Because green and yellowish fruit are usually unripe and half-ripe stages in the development of fruit and also do not contrast with the leaves as much as red ones, many birds will probably not detect T. natalitius fruit easily and if they did, would possibly ignore them. Hence, for birds, T. leendertziae has visually the most attractive fruit of the three species. Furthermore, the fruit of T. leendertziae has the softest exocarp when ripe; its seed being relatively easy to remove from the fruit.

During March 1977 the largest number of observations of birds feeding on the fruit of T. leendertziae was obtained, as well as the widest variety of birds eating its fruit (seven species); the contribution of the Yellowfronted Tinker Barbet being only 52% (Appendix 3). In that season a very good crop of T. leendertziae fruit was available, all the plants being covered by a mass of bright red fruit. During the 1978 season, however, a poor crop was produced (see Section 4.1.3.1). Six avian species fed on fruit of T. leendertziae, with the contribution of the Yellowfronted Tinker Barbet being 81%. Thus, it seems that when a good crop of T. leendertziae fruit is available, "non mistletoe specialists" take relatively more fruit. During seasons of moderate or poor crops, however, the "mistletoe specialist" Yellowfronted Tinker Barbet is the main eater of the fruit of T. leendertziae.

The low number of feeding records pertaining to T. natalitius is, among other factors, attributable to the low number of ripe fruit available on a plant at any one time (see Section 4.1.3.1). The high number of feeding records pertaining to V. combreticola is due to the plant's continuous production of fruit throughout the year.

Because I spent relatively little time making observations at V. rotundifolium plants, I recorded only two avian species eating its fruit. As the fruit of V. rotundifolium, the smallest of the five mistletoe species in the reserve, seems to be structurally most suitable for dispersal by a wide variety of birds, it is likely that additional species in the camp (the only place where V. rotundifolium was available in fair numbers) also fed on V. rotundifolium fruit as they were observed elsewhere to do so.

Details attending the distribution of the feeding records for each species of mistletoe-eating bird are shown in Appendix 3. Appendix 4 includes a complete list of all southern African records of mistletoe-eating birds, known to me, and the mistletoe species on whose fruit they fed. An account of the other fruit-eating birds in the area, with remarks on their relation to mistletoes, is given in Appendix 6.

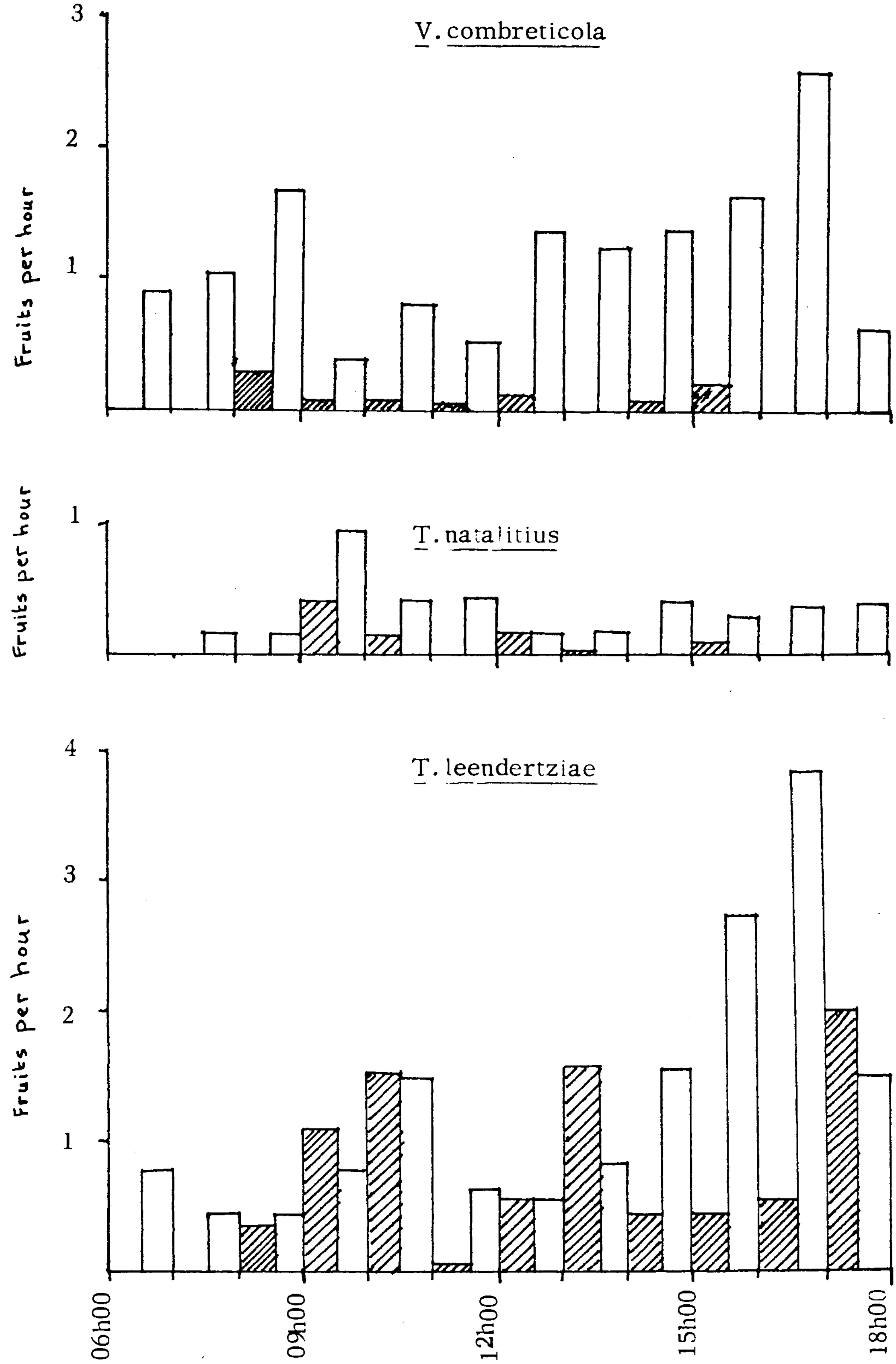


Figure 9. Diurnal variation in rate of removal of fruit of three mistletoe species by birds in he Loskop Dam Nature Reserve. Unshaded columns indicate records for Yellowfronted Tinker Barbets, and shaded columns records for all other bird species. Based on 198h, 193h and 538h of observations on Tapinanthus leendertziae, T. natalitius and Viscum combreticola, respectively

4.2.2 Rate and time of removal of mistletoe fruit by birds

Figure 9 shows the diurnal variation in the rate at which the fruits of the three mistletoe species were removed by birds. The overall rate of removal of fruit of Tapinanthus leendertziae was 2,1 fruits/h. A minor peak in the birds' feeding occurred between 10h00 and 11h00, but the rate increased steadily from the lowest figure, at noon, throughout the afternoon to reach a major peak between 16h00 and 17h00. This pattern was particularly clear for the Yellowfronted Tinker Barbet. In the other bird species no definite pattern could be observed (which applies to all three species of mistletoe). This can be explained by the variety of birds involved, which were only incidental feeders on mistletoe fruit (see Section 4.2.1). As some of these birds feed mostly in small flocks, the records for three of the four periods of relatively high removal rates for "non tinker barbets" were mainly due to single visits by a relatively large number of individuals of one species.

The overall rate of removal of fruit of T. natalitius was low (0,4 fruits/h), which can largely be ascribed to the low number of ripe fruit available on a plant at any one time (see Section 4.1.3.1). The feeding records are distributed rather evenly throughout the day, except for the very low rate of removal in the early morning (presumably among other things caused by the relatively short days and cold early mornings during autumn and winter) and one peak between 09h00 - 10h00. The "non tinker barbet" part of this peak was contributed entirely by a single visit of four Black Tits on 23 March 1977.

The overall rate of removal of fruit of Viscum combreticola was 1,2 fruits/h. The removal rate during February - June, when Tapinanthus fruit was available, was considerably lower (0,61 fruits/h) than during the rest of the year, when only V. combreticola fruit was available (1,62 fruits/h, see Fig.10) (July is included because of the very low and diminishing number of T. natalitius fruit available during that month). The reason for the unusually high rate of removal during September and the very low rate for November is not clear. However, the observed change in feeding on V. combreticola fruit seems to be related to fruit availability. During July - January the feeding pressure on V. combreticola fruit is high, for it is the only mistletoe fruit available. This results in a high rate of removal of fruit (Figure 10) and a low number of ripe fruit available during that period (Fig. 8, see Section 4.1.3.1). When Tapinanthus

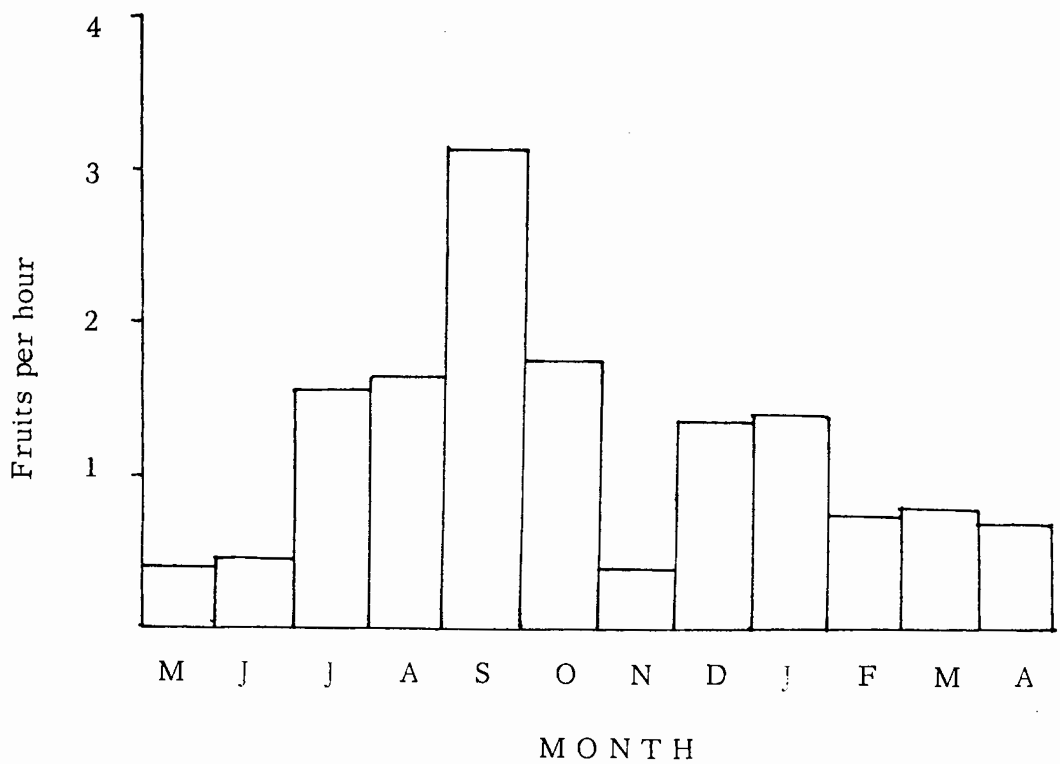


Figure 10. Rate of removal of fruit of *Viscum combreticola* by birds, in the Loskop Dam Nature Reserve during May 1977 - April 1978. Based on 538h of observations

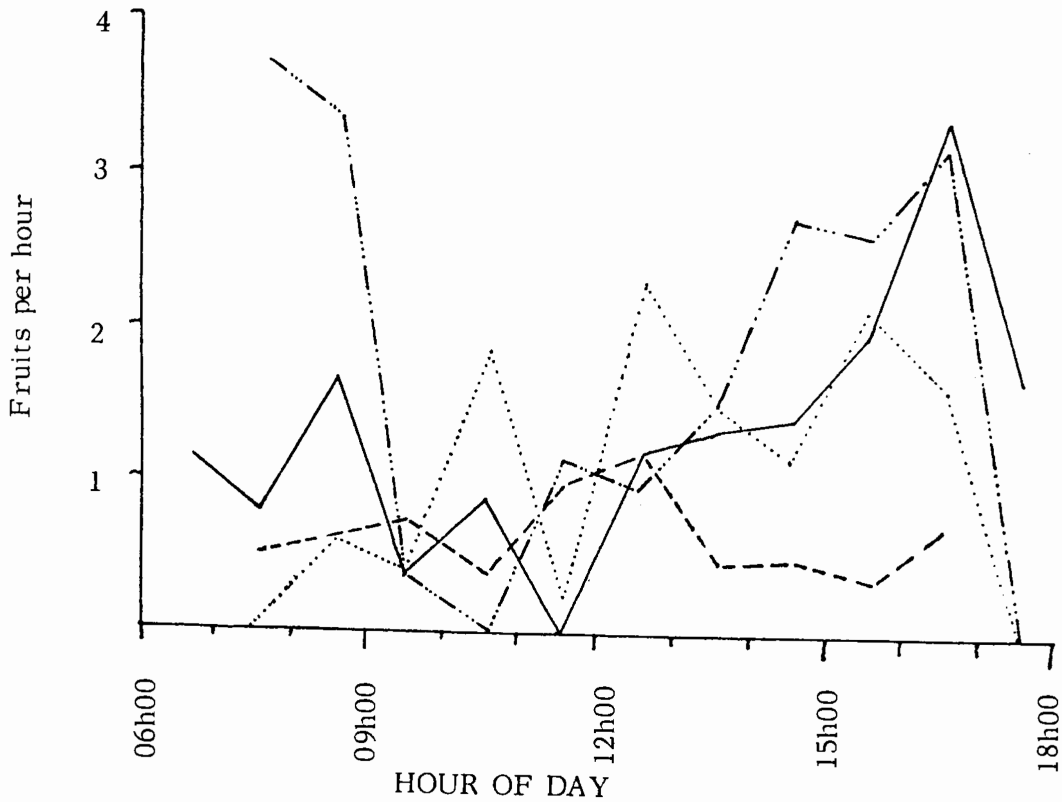


Figure 11. Diurnal variation in rate of removal of fruit of Viscum combreticola by birds in the Loskop Dam Nature Reserve during spring (-·····-····; September-November), summer(————; December-February), autumn (– – – – –; March-May) and winter (··········; June-August)

fruit becomes available, tinker barbets shifted partly to that fruit, thereby relieving the high feeding pressure on V. combreticola fruit, and consequently more ripe fruit of V. combreticola was observed during this period (Fig. 8, see Section 4.1.3.1).

Seasonal variation in the diurnal rate of removal of fruit of V. combreticola is shown in Figure 11. During autumn and winter the main consumption of fruit took place between 10h00 and 16h00. This is partly related to the relatively short days, and probabl y also to the lower ambient temperatures which allow the bird to be more active during the middle of the day wihtout dan ger of heat stress. In spring (which is quite warm, particularly when rains are still absent) and summer, most feeding activity was undertaken during the cooler mornings and late afternoons, presumably, among other things, to avoid heat stress. The same explanation probably pertains largely to the pattern observed for T. leendertziae. The major peak in the rate of removal of fruit of T. leendertziae and V. combreticola during the late afternoon (higher than the morning peak) is explained as increased feeding to obtain food for the long night ahead (about 10 - 12 hours during which no feeding is possible). The period for which food has to be taken during the morning feeding session, is shorter, and the birds are able to, and actually do, feed between the two main feeding sessions. The even distribution of the rate of removal of T. natalitius fruit is probably related to the relatively low number of fruit available at any one plant. Because fruit were taken at a steady rate throughout the day - probably allowed by the relatively low ambient temperatures during the period of its fruit availability (see above) - insufficient fruit were left towards the end of the day to permit an increase in the rate of removal.

The overall rates of removal of mistletoe fruit by birds appear to be related to the number of fruit available on a plant at one particular time. During the exceptionally good fruit crop of T. leendertziae during March 1977 (see Section 4.1.3.1), the rate of removal of its fruit was as high as 3,2 fruits/h, while during the poorer 1978 season it was 1,4 fruits/h. The rate of removal of fruit of T. natalitius, which has few fruit available per plant at any one time, was only 0,4 fruits/h, and for V. combreticola, with a moderate number of fruit available at any one time, it was 1,2 fruit/h.

4.2.3 Aspects of the feeding of birds on mistletoe fruit

4.2.3.1 Methods used by birds in dealing with the various parts of mistletoe fruit

Birds were observed to deal with the various parts of mistletoe fruit in three main ways. The most important method (hereinafter called the "regurgitation method") was used by Blackcollared and Pied barbets, Yellowfronted Tinker Barbets and Plumcoloured Starlings, which together accounted for 92% of the records for avian consumption of fruit of the three common mistletoe species in the study area (see Table 2).

The fruit is plucked, and squeezed between the mandibles. When the exocarp cracks the fruit is aligned in such a way that the content slips into the bird's mouth, and the exocarp is discarded. The whole process usually lasts less than 10 seconds. Usually within one minute (see Section 4.2.3.4), the seed is regurgitated and sticks to the beak, because of the sticky viscin. Subsequently, the seed is wiped off onto the branch on which the bird is sitting. The aril has previously been removed in the bird's alimentary tract, providing the bird with food and facilitating contact later between the viscin and the branch.

The Plumcoloured Starling was once observed to regurgitate red packets and to drop them to the ground. These packets consisted of remains of red arils of T. leendertziae fruit. In captivity, the tinker barbet ate the fruit of V. rotundifolium usually wholly, but it always discarded the exocarps of the fruit of V. combreticola and both Tapinanthus species; the seeds of all four species of mistletoe were always regurgitated. Small pieces of apple were regurgitated, too, and then wiped off the beak. Captive Blackcollared Barbets regurgitated and defaecated seeds of V. combreticola and V. rotundifolium but those of T. natalitius were only regurgitated. Seeds of Clerodendron glabrum, Ehretia rigida, Ficus burkei and F. capensis were defaecated by these birds, whereas those of Euclea crispa were either regurgitated or defaecated. Captive Crested Barbets defaecated seeds of V. rotundifolium and V. combreticola, whereas those of T. natalitius were mostly regurgitated (Godschalk 1976). Seeds of Clerodendron glabrum and Ficus capensis were only defaecated, whereas those of Euclea crispa were either regurgitated or defaecated. The Goldenrumped Tinker Barbet was observed to regurgitate the seeds of Erianthemum dregei in Natal, but often it just drops the seeds without planting them (see Section 5.3).

The only previous description of the regurgitation method in African birds eating mistletoe fruit was given by Cowles (1959) for the Redfronted Tinker Barbet in Natal. These records of regurgitation of mistletoe seeds in other continents could be traced. Gosse (1847,quoted by Ridley 1930) once observed a Redeyed Vireo Vireo olivaceus, in Jamaica, to "vomit" a single mistletoe seed (probably of Phoradendron, a viscoid species). Brittlebank (1908) reported that the Grey Bell-Magpie Strepera versicolor in Australia "casted" seeds of Loranthus exocarpi together with other food remains in the form of pellets which, however, from their nature, only rarely adhered to a branch. The same bird is also reported to defaecate Loranthus seeds (Blakely 1922). Several tyrant-flycatchers (family Tyrannidae) are reported to regurgitate mistletoe seeds in Panama (Leck 1972).

The second method (hereinafter called the "defaecation method") was used by Speckled and Redfaced mousebirds feeding on the fruits of V. rotundifolium and V. combreticola, respectively. The fruit were eaten wholly, and the seeds were defaecated in packets, followed by packets of exocarps. Many of these packets just dropped to the ground. If they adhere to a branch, they often form strings hanging down from the branch. Strings of defaecated seeds of T. leendertziae, similar to those of Viscum seeds produced by mousebirds were found several times in the field, indicating that mousebirds (the Redfaced Mousebird was observed feeding on fruit of T. leendertziae) might defaecate the seeds of Tapinanthus, too. Captive Blackeyed Bulbuls, Kurrichane and Olive thrushes and Cape White-eyes, all defaecated seeds when fed fruit of V. rotundifolium (Godschalk 1976). The defaecation of mistletoe seeds has been reported from all continents in a wide variety of birds (see Section 5.4.).

Southern Black Tits and Redheaded Weavers were observed to use a "pecking method" in feeding on Tapinanthus fruit. The fruit is plucked and squeezed. When the exocarp cracks, the content is taken into the bird's beak and the exocarp is discarded. The "arillate seed" is then placed onto a branch, and the bird pecks off pieces of the aril until most of it has been removed. During this procedure, the seed is held in position by the feet of the bird which sometimes also uses its beak in realigning the "seed". After most of the aril has been removed, the seed sticks to the branch by means of the viscin. The only description of similar behaviour, performed by birds while eating mistletoe fruit, is found in Heim de Balsac and Mayaud (1930) for the Blackcap Sylvia atricapilla feeding on V. album fruit in France. In this case, after cracking the exocarp, the whole fruit is placed onto a branch, after which both the exocarp and the pulp are removed and swallowed, leaving the seed attached to the host branch.

The regurgitation method is used by the most important mistletoe-eating birds. Nearly every seed, planted in this way, is attached to a host branch. In fact, I observed only twice that a seed, regurgitated and planted by the Yellowfronted Tinker Barbet, had not been firmly attached; the seed had dropped to the ground. This was also occasionally observed in Blackcollared Barbets regurgitating seeds of V. combreticola which was probably caused by the small size of the seed in relation to the large beak of this barbet. Because the ballast weight of the seeds is not carried far by the birds, but is removed rather quickly (see Section 4.2.3.4), more fruit can be handled per unit time. resulting in a higher rate of intake of nutritious food. As the aril is removed completely in the alimentary tract, the short time the seeds remain there probably does not decrease the actual intake of food.

Many seeds drop to the ground when they are defaecated, and are therefore wasted. If the defaecated seeds are attached to a branch, they often hang down in strings. Consequently, only the uppermost seeds are in contact with the branch, and are able to form new plants. If the whole packet of seeds were to be placed on a branch, this would result only in one effective plant (even if consisting of a cluster of a few individual plants). A very high proportion of the seeds is thus wasted when they are defaecated. Because only a part of the aril is removed during the pecking method, the attachment of the seed to the host branch is probably not as firm as in regurgitated seeds, resulting in relatively more seeds dropping to the ground.

The food reward is at least as high in the defaecation method as in the regurgitation method, possibly even somewhat higher (if, possibly, part of the viscin layer is digested too, a subject for which no data are available), but the ballast weight and volume of seeds are carried around for a longer period. The food reward per fruit is not as high in the pecking method because the aril is not removed completely. No ballast of seeds is, however, carried around by the bird.

The major disadvantage for the plant in the regurgitation and pecking methods is the relatively short distance of dispersal. In the pecking method, seeds are usually deposited either on the parent mistletoe plant, its host or a neighbouring tree. The short retention time of seeds before regurgitation (see Section 4.2.3.4), also results usually in a short distance of dispersal, often no farther than the same mistletoe plant or its host. Because seeds remain in the alimentary tract for a longer time in the defaecation method, the distance over which they are carried is potentially much longer than in the other methods.

In conclusion, the regurgitation method is most effective from the bird's viewpoint, because it gives the highest food reward per unit time and unnecessary, extra-energy demanding ballast is carried around for a relatively short period. From the plant's viewpoint, it is the most reliable method of dispersal, because nearly all seeds are planted securely on branches. The distance of seed dispersal is, however, relatively short in the regurgitation method, so that, whereas the defaecation method is used only with a small fraction of all the mistletoe seeds (and most of them are presumably wasted), it may still be important for long-distance dispersal. The defaecation method is probably of more importance in the case of the smaller-seeded Viscum species, like V. capense and V. rotundifolium, the fruit of which are presumably eaten by a wider variety of birds. Among these birds, the following species have been recorded to eat the fruit and defaecate the seeds of V. rotundifolium: Speckled and Redfaced mousebirds, Blackcollared (most seeds defaecated) and Crested barbets, Blackeyed Bulbuls, Kurrichane and Olive thrushes and Cape White-eyes (Bunning in litt. 1978; Godschalk 1976, and this study).

The process, mentioned in the South African botanical literature (see Section 2), whereby the seed is wiped off the beak during handling of the fruit, was not observed during this study. As no detailed description of the behaviour is given in the literature, it is not clear how many of the references are based on actual observation or whether some of them refer to the wiping of the seed off the beak after regurgitation. It is possible, because of the viscous nature of the contents of mistletoe fruit, that sometimes a seed will stick to the bird's beak while the bird is feeding, and will be wiped off, but this occurs probably only incidentally. As no food is taken in during this process, it is unlikely that its occurrence is of a regular nature. It is even more unlikely that birds will fly around with these seeds stuck to their beaks, and deposit the seeds far from the parent plant (as suggested by Van Hoepen 1968).

The factors determining whether a seed is regurgitated or defaecated, are not completely clear. The size of the seeds and the birds involved, as well as the nature of the bird's alimentary tract, are probably important. The smallest mistletoe-eating bird, the Yellowfronted Tinker Barbet, regurgitated all mistletoe seeds. The larger Tapinanthus seeds were regurgitated by the Blackcollared and Crested barbets, whereas they defaecated most or all of the smaller Viscum seeds. That seed size influences the way in which the seed is dealt with by birds was also found by Ranger (1950) in the Crowned Hornbill Tockus alboterminatus. This species regurgitated most seeds, but sometimes a few of the smaller seeds escaped into the intestine, and were defaecated. Oatley (1970) reported that all seeds larger than 2mm were regurgitated by 22 species of robins (Family Turdidae). However, whereas the larger barbet species (Blackcollared, Pied and Crested), as well as the relatively large Plum-coloured Starling, regurgitated the seeds of Tapinanthus, the smaller mousebirds probably defaecated them. Possibly the alimentary tract of the specialist fruit-eating mousebirds is wider than in the partly insectivorous barbets and starling, permitting the larger Tapinanthus seeds to pass easily through. Why some seeds of V. combreticola were regurgitated and others defaecated by the same Blackcollared Barbet at the same time is not clear.

4.2.3.2 Stages at which mistletoe fruit are eaten by birds

Tapinanthus leendertziae

In this species, fruit in the red stage usually were eaten by birds. However, the Blackcollared Barbet and the Plumcoloured Starling were observed occasionally to feed on greenish fruit. In the case of the Plumcoloured Starling, however, the aril of the fruit was already red (its colour in the ripe state). Sometimes orangish fruit were eaten.

Tapinanthus natalitius

The maturity of this mistletoe's fruit is not always easy to discern visually, as the fruit become ripe while still green. Most fruit observed to be eaten by birds were green or yellowish-green. Few fruit reached the final, red stage, of maturity. The slow rate of fruit development results in a low number of ripe fruit available on a plant at any one time (see Section 4.1.3.1). Therefore, the fruit are removed as soon as they ripen, so that few are allowed to become red. Apparently, the Yellow-fronted Tinker Barbet is able to discern visually with some accuracy the green ripe fruit, though sometimes green fruit were probed by the birds in testing for ripeness (this was not observed in the case of fruit of the other mistletoe species). Sometimes, even fruit which had already been plucked, were dropped, apparently being too hard (unripe). Of 53 exocarps collected on the ground under a tree hosting two large and one small T. natalitius plants (the ground had been cleared thoroughly 11 days earlier), 31 were green, 21 yellowish-green and only one showed signs of red coloration. This reflects fairly accurately the stages at which the fruit are eaten.

Viscum combreticola

Most of the fruit of this mistletoe were eaten when reddish. Yellowfronted Tinker Barbet was observed eating greenish-orange fruit on a few occasions, which all occurred during August - October, when relatively few red fruit was available (see Section 4.1.3.1).

4.2.3.3. The number of mistletoe fruits taken per feeding bout by birds

A feeding bout was defined as the number of fruits taken consecutively before the bird started regurgitating the seeds. Table 13 shows the number of fruits of the three mistletoe species taken per feeding bout in the field by the four species of birds which use the regurgitation method.

Captive, individual Blackcollared Barbets once consumed five and seven fruits of V. combreticola per feeding bout, respectively, and on occasions similar numbers were taken as by wild birds in the field. Once seven fruits of V. rotundifolium were taken at once, whereas the average feeding bout on Euclea crispa fruits was 2,2 (1-3; n=5) for this bird. The average number of fruits taken per bout by a captive Yellowfronted Tinker Barbet was similar to that observed in the field.

The number of fruits per feeding bout seems to be related to the size of the bird, as well as to the size of the seeds involved. The smallest numbers of fruits per feeding bout were usually observed in the Yellowfronted Tinker Barbet, which is the smallest mistletoe fruit eater. The largest number of fruits per feeding bout for T. leendertziae was found in the Plumcoloured Starling, the largest of the four bird species involved, which took as many as twice the number of fruits per feeding bout as the barbet species. As the time intervals between consecutive regurgitations of seeds following one feeding bout were relatively short (see Section 4.2.3.4), it is likely that the seeds derived from any particular feeding bout, will be deposited closer to each other than seeds of different bouts. The Plumcoloured Starling, particularly, was observed several times to deposit

Table 13. The number of fruits of three mistletoe species taken per feeding bout by four species of birds in the Loskop Dam Nature Reserve

	Species of mistletoe		
Species of bird	T. leendertziae mean (range) N	T. natalitius mean (range) N	V. combreticola mean (range) N
Blackcollared Barbet	2,6 (2-4) 5	2,0 (1-3) 4	3,8 (3-4) 4
Pied Barbet	3,2 (2-4) 6	2,0 (2) 1	3,0 (3) 1
Yellowfronted Tinker Barbet	1,9 (1-3) 102	1,6 (1-3) 28	3,2 (1-5) 65
Plumcoloured Starling	4,5 (1-8) 13	-	-

neat rows of about six seeds next to each other. This is presumably disadvantageous for the plant, since it probably results in direct competition between the propagules for the same host branch. Smaller numbers of fruits per feeding bout presumably results in less dense dispersion of seeds, and thus reduced competion between future mistletoe plants. In this respect the Yellowfronted Tinker Barbet is the most suitable dispersor of the four avian species which regurgitate the seeds. The maximum number of fruits of T. leendertziae taken per feeding bout by the Yellowfronted Tinker Barbet was three, the content of which together weighed 0,77 g (wet weight) or 6,2% of the bird's body weight.

The feeding bouts involving fruit of T. natalitius (which has the largest seeds), were smallest, whereas those involving fruit of V. combreticola (which has the smallest seeds) were largest (Table 13). This is explained by the fact that the capacity of the birds' stomachs apparently is limited, permitting accommodation of fewer larger seeds and more smaller seeds at one time. This probably leads to a relatively clustered deposition of seeds in the case of V. combreticola, which agrees with the fact that large clusters of V. combreticola plants were encountered regularly in the field. Clustered deposits of Tapinanthus seeds, on the other hand, were found infrequently in the field. The number of fruits per feeding bout hardly influenced the amount of time spent by the bird on "handling" individual fruits (see Section 4.2.3.4, Table 15), and thus did not affect "handling" efficiency.

During visits to Tapinanthus plants, the Yellowfronted Tinker Barbet was never observed to eat more than eight fruits per visit, which usually lasted a few minutes at most (the mean duration of 21 visits to T. leendertziae plants was 3,1 min (1-10, n=19) in T. natalitius it was 2,2 min (1-6, n=14). In contrast, visits of more than 30 minutes to V. combreticola plants were recorded several times (mean duration of visits 12,1 min (1-57, n =30), and as many as 40 fruits were consumed. During these long visits most seeds were deposited on the same host (see Section 4.2.5), which undoubtedly contributes to the above-mentioned clustering of V. combreticola plants, too.

There appears to be no direct relation between the number of ripe fruit available on a plant and the duration of a bird's visit to it, though the shortest visits were paid to T. natalitius plants which have the lowest number of fruit available at any time. In the case of T. leendertziae, tinker barbets usually terminated their visits after feeding on a few fruits of plants full of ripe fruit, and these plants were visited more regularly than plants of V. combreticola. This indicates that the birds moved around more between visits to mistletoes while feeding on T. leendertziae than while feeding on V. combreticola. Moving around between visits to mistletoe plants may be advantageous to the bird, since predators would probably be attracted more easily by prolonged activities at one plant. On the other hand, it may be that individuals or clusters of V. combreticola are relatively sparsely distributed. Furthermore, a certain proportion (e.g. 32% of the plants involved in the phenological survey) of V. combreticola plants are male individuals which do not bear fruit at all. This possibly results in a relatively low number of plants bearing fruit in a particular area, which would cause the bird to pay relatively long visits to single plants.

A few observation are available for those avian species which do not regurgitate seeds. Once a Redfaced Mousebird was observed to consume 10 fruits of T. leendertziae within three minutes, which gives an indication of the bird's food-storing capacity. Flocks of mousebirds sometimes spent long periods feeding and resting in mistletoe plants, resulting in many seeds being defaecated on, under or close to the plants. Southern Black Tits and Redheaded Weavers usually departed after feeding on at most five fruits.

4.2.3.4. Time mistletoe seeds were retained by birds

"Handling" time was defined as the time between the swallowing of a fruit and the depositing of the seed by a bird if one fruit was taken; if more than one fruit was taken, it was defined as the time between the swallowing of the first fruit and the depositing of the last seed divided by the number of fruits eaten per feeding bout. Table 14 gives the mean duration of different components of the "handling" procedure of mistletoe fruit by the four bird species which regularly regurgitated seeds. The Yellowfronted Tinker Barbet is the most efficient mistletoe fruit eater, handling fruit of T. leendertziae faster than the two other barbet species. The Plumcoloured Starling showed a similar speed of handling, influenced mainly by a relatively fast rate of consumption of fruit. In the case of T. natalitius the tinker barbet handled fruit faster than the Blackcollared Barbet, but apparently slower than the Pied Barbet (which, however, may be incorrect, since the data for the Pied Barbet are not sufficiently representative). The tinker barbet handled V. combreticola fruit faster than both other barbet species.

Table 14. Mean duration (sec) of different components of the handling procedure of fruit of three mistletoe species by four species of birds which regurgitate seeds, in the Loskop Dam Nature Reserve

Bird species	Mistletoe species	Component 1 mean (range) N	Component 2 mean (range) N	Component 3 mean (range) N
Blackcollared Barbet	T.l.	26,0 (19-37) 5	39,0 (31-47) 2	34,5 (29-45) 4
	T.n.	30,0 (22-38) 2	77,7 (45-120) 3	36,0 (28-40) 3
	V.c.	13,9 (7-22) 8	35,0 (35) 1	26,7 (19-36) 3
Pied Barbet	T.l.	26,5 (21-33) 4	37,0 (35-41) 3	38,6 (10-90) 10
	T.n.	19,0 (19) 1	43,0 (43) 1	31,0 (31) 1
	V.c.	17,0 (12-22) 2	31,0 (31) 1	25,0 (18-32) 2
Yellowfronted Tinker Barbet	T.l.	16,7 (6-31) 47	36,4 (18-100) 37	21,6 (10-43) 34
	T.n.	18,4 (14-29) 9	58,2 (26-153) 11	43,4 (16-115) 5
	V.c.	14,4 (3-32) 103	22,8 (12-48) 44	19,1 (5-53) 95
Plumcoloured Starling	T.l.	9,3 (5-13) 15	48,8 (35-60) 4	21,9 (5-50) 26

T.l. = Tapinanthus leendertziae
T.n. = T. natalitius
V.c. = Viscum combreticola

Component 1 = interval between swallowing of consecutive fruits in a feeding bout
Component 2 = interval between swallowing of the last fruit in a feeding bout, and regurgitation of the first seed
Component 3 = interval between regurgitation of consecutive seeds in a feeding bout

The handling time per fruit was related to the size of the seed involved. Fruit of T. natalitius (which has the largest seed) were handled slowest, whereas fruit of V. combreticola (which has the smallest seed) were handled fastest. The extra-proportionally slow speed of handling of T. natalitius fruit (see particularly the data for the tinker barbet in Table 14) is probably bound up with the tough pellicle (aril), which is more difficult to remove than the fragile aril of T. leendertziae. In the case of V. combreticola, the smallness of the seed, as well as the jelly-like nature of the aril, probably facilitate fast handling. The relatively high speed of handling of mistletoe seeds (between 30-60 sec/seed) suggests that the aril is removed mechanically, presumably in the stomach of the bird.

Data on handling time and feeding bout (see Section 4.2.3.3) for the Yellowfronted Tinker Barbet were correlated (Table 15), showing that handling time per fruit is possibly slightly reduced if only one fruit is taken per feeding bout, but otherwise variation in feeding bout has virtually no influence on the speed at which individual fruits are handled.

Limited observations made on captive birds (see Appendix 7) indicate slower handling speeds than those obtained for birds in the wild. The reasons for the slower handling speeds per fruit in the captive birds are not entirely clear. According to Keast (1958), the passage of seeds through the alimentary tract will be faster in free-living birds, as they are more active. Frost (pers. comm.) suggested that the regurgitated seeds may have been swallowed during a former feeding bout. For several reasons, however, this seems improbable in the case of the Yellowfronted Tinker Barbet. The regurgitation of seeds within a minute or so after the swallowing of mistletoe fruit was so consistent and, furthermore, in the light of the small size of the bird, and consequently the apparently limited capacity of its stomach, it seems unlikely that a bird would commence a bout of feeding, while the seeds of the last bout are still in its stomach. I regularly observed that tinker barbets, after having swallowed a certain number of fruit, would sit quietly until the seeds had been regurgitated, before beginning to eat again. Experiments with colour-marked seeds would be necessary in order to resolve the problem definitely.

I was unable to find precise information on the handling time of fruit by species of

Table 15. Mean duration (sec) of different components of the handling procedure of fruit of three mistletoe species by the Yellowfronted Tinker Barbet in relation to number of fruits per feeding bout (see Table 14 for definitions of components 1-3)

Mistletoe species	No. fruits per bout	Component 1 mean (N)	Component 2 mean (N)	Component 3 mean (N)	Mean handling time per fruit
T. leendertziae	1	-	33,4 (12)	-	33,4
	2	18,3 (27)	37,8 (19)	21,5 (20)	38,8
	3	14,7 (20)	40,3 (6)	21,6 (14)	37,6
T. natalitius	1	-	57,0 (6)	-	57,0
	2	15,8 (5)	49,3 (4)	60,0 (3)	62,6
	3	21,3 (4)	101,0 (1)	18,5 (2)	60,2
V. combreticola	1	-	24,5 (2)	-	24,5
	2	13,7 (15)	25,3 (12)	20,4 (9)	29,7
	3	14,7 (22)	19,7 (10)	20,4 (16)	30,0
	4	15,5 (41)	22,7 (15)	17,7 (43)	30,6
	5	12,1 (16)	23,0 (3)	20,1 (16)	30,4

birds known to regurgitate seeds, except for Ranger's (1950) statement that seeds of Commiphora, Royena and Scutia ("which are held loosely by adherent tissue") were "cast within half an hour of being swallowed" by the Crowned Hornbill Tockus alboterminatus.

The relatively short retention time of mistletoe seeds in the guts of birds points to potentially fast rates of removal of fruit (about 90 fruits/h in T. leendertziae, 60 fruits/h in T. natalitius and 120 fruits/h in V. combreticola). The roughly approximated number of fruits of T. leendertziae needed to satisfy the daily energy requirements of a Yellowfronted Tinker Barbet (172 fruits, see Section 4.1.6), could be consumed in two hours of continuous feeding. The rapid regurgitation of seeds results, however, in deposition of the seeds relatively close to, and often on the same host, as the parent plant. This is disadvantageous to the plant because of enhanced competition for available hosts, and possibly because it might promote higher species-specific predation near the parent plant. The relatively short retention time of seeds of V. combreticola together with the large number of fruits taken per feeding bout and the longer visits of birds to this mistletoe's plants (see Section 4.2.3.3), are probably to a large extent responsible for the clusters of V. combreticola plants, so often observed in the field.

The processing time of fruit of T. leendertziae by the Southern Black Tit averaged 27,7 sec per fruit (20-38; n=9); in the Redheaded Weaver it once was 45 sec . The time between swallowing and defaecation of mistletoe seeds by mousebirds could not be measured in the field. Captive Crested Barbets defaecated seeds of V. rotundifolium after an average time of 17,7 min (8-38; n=78); for Blackeyed Bulbuls the corresponding figure was 18,5 min (5-34; n=128), and for a Kurrichane Thrush 23 min (one feeding bout of six fruits) (Godschalk 1976). The Yellowfronted TInker Barbet did not defaecate any seeds. The Blackcollared Barbet defaecated seeds of V. combreticola after about 22 min (10-35; n=10), and those of V. rotundifolium after about 24 min (18-33; n=6). Two seeds of Ehretia rigida were defaecated after 32 min by this bird, and seeds of Euclea crispa were defaecated after 18,6 min (14-30; n=7). Though some seeds were defaecated after 5 min, seeds of V. combreticola and V. rotundifolium apparently were defaecated on average after a longer period than those of some Indian mistletoes. Ali (1931) reported that seeds of Dendrophtoe falcata (a viscoid species) were defaecated after only 3-4 min by Tickell's Flowerpecker Dicaeum erythrorhynchos, while Ryan

(1899, quoted by Docters van Leeuwen 1954) reported seeds of Loranthus longiflorus to be defaecated after 8-12 min by the same species of bird. This species' rapid defaecation of mistletoe seeds is explained by the extraordinary intestinal tract found in several members of the genus Dicaeum (Dammerman 1929; Desselberger 1931; Mayr & Amadon 1947; Docters van Leeuwen 1954), where the gizzard is a blind sac with a sphincter at its opening. Only insect food enters the gizzard, whereas mistletoe seeds are shunted directly from the oesophagus to the intestine without entering the gizzard. This causes the seeds to pass rapidly through the alimentary tract. Passing times of mistletoe seeds were 12 min (n=3) and 22 min (n=6) in the Javan Firebreasted Flowerpecker Dicaeum sanguinolentum (Docters van Leeuwen 1954); 25-60 min in the Swallow Mistletoebird D. hirundinaceum and 30-80 min in the Australian Silvereye Zosterope lateralis (Keast 1958); 29 min (range 12-45 min) in the Western Silky Flycatcher (or Phainopepla) Phainopepla nitens (Walsberg 1975b); and about 30 min in the Mistle Thrush (Tubeuf 1923, quoted by Kuyt 1969). The Bohemian Waxwing Bombycilla garrulus defaecated seeds of Viscum album 6-31 min after swallowing (50% were defaecated after 14,5 min, Borowski 1966). By comparison, in the same bird 50% of the seeds of the snowberry Symphoricarpos albus, the service tree Viburnum opulus and the wayfaring tree Sorbus aucuparia were defaecated after 13,5, 25,0 and 27,5 min, respectively (Borowski 1966). The time between swallowing and defaecation of Viscum seeds in South African birds is thus roughly similar to what has been reported for a variety of other mistletoe fruit-eating birds.

The relatively long (in comparison with regurgitated seeds) retention time of mistletoe seeds before defaecation allows deposition of seeds at much longer distances from the parent plant. Therefore, for relatively long-distance dispersal, mistletoes (especially Viscum species) are probably mostly dependent on birds defaecating the seeds. The defaecation method has, however, certain serious disadvantages which have been discussed in Section 4.2.3.1.

4.2.4 Interactions between birds feeding on mistletoe fruit

Interspecific interactions

Yellowfronted Tinker Barbets were observed feeding together with Redfaced Mousebirds, a Pied Barbet and a Plumcoloured Starling at T. leendertziae plants. On two occasions, I observed Yellowfronted Tinker Barbets feeding together with Blackcollared Barbets, also at T. leendertziae plants. On one occasion two tinker barbets and four Southern Black

Tits were observed feeding together at a T. natalitius plant. In all these cases, no aggressive interspecific behaviour was observed between the birds. Five of the interspecific feeding associations were observed at T. leendertziae plants, one at a T. natalitius plant and none at V. combreticola plants, which correlates well with the variety of birds feeding on the fruit of the different mistletoe species (see Section 4.2.1). Once a Forktailed Drongo Dicrurus adsimilis, which was a member of a passing bird party, vigorously chased a Yellowfronted Tinker Barbet which was feeding on T. natalitius fruit. On one occasion a tinker barbet flew to a neighbouring tree when a Striped Kingfisher Halcyon chelicuti arrived at the tree where the tinker barbet was feeding on V. combreticola fruit. The tinker barbet returned after the kingfisher had flown away.

Intraspecific interactions

Individual Yellowfronted Tinker Barbets normally fed alone. Two birds feeding together (observed on 14 occasions) was the maximum number I observed. Aggressive behaviour was observed during 9 of these 14 two-bird associations. The birds made a typical "churring" sound, and chased each other. Nine of the two-bird associations were observed at T. natalitius plants (during six of which aggressive behaviour was observed), three at T. leendertziae plants (two aggressive encounters) and two at V. combreticola plants (one aggressive encounter). There seems to be no difference in the proportion of aggressive encounters at plants of the different mistletoe species, but the actual number of intraspecific encounters seems to be inversely related to the duration of visits to plants of the different mistletoe species (see Section 4.2.3.3). Shorter visits are presumably related to more wandering about, which increases the chance of encounters. On two occasions a tinker barbet was observed to feed mistletoe fruit to its associate; in one case the associate was a female fed by a male (copulation was observed).

In conclusion, the number of aggressive interactions between birds feeding on mistletoe fruit was relatively low. Yellowfronted Tinker Barbets showed no aggressive behaviour towards other bird species but only towards members of their own kind. Not much has been published regarding social organization or territorial behaviour in barbets, including tinker barbets. Skead (1950) observed aggressive behaviour against intruding conspecifics in Blackcollared Barbets, and pairs which he studied, held territories for several years. A male Crested Barbet reacted very aggressively when I brought a captive male conspecific into its territory. Presumably most barbets and tinker barbets are territorial. There were some indications that Yellowfronted Tinker Barbets hold territories throughout the year in the study area. When I played a tape-recording of its call, a tinker barbet, if it was in the vicinity, would invariably come close to me and start calling. Often it flew vigorously in the direction of the tape-recorder, as if to drive off the "intruder". This behaviour was observed at any time of the year. Furthermore, two of the aggressive encounters between tinker barbets were recorded during March (at T. leendertziae plants), three during May and June, respectively (T. natalitius), and one during October (V. combreticola), indicating that aggressive behaviour was not at all restricted to the bird's breeding season, which occurs during September - December in the Transvaal (Winterbottom 1971). As indicated above, the number of intraspecific interactions was related to the length of the visits to plants of the three mistletoe species. The above-mentioned findings, together with the fact that never more than two tinker barbets were seen together, suggest that pairs of Yellowfronted Tinker Barbets hold territories throughout the year within which they may obtain their food (which is facilitated by the year-long availability of mistletoe fruit), and from which they apparently exclude conspecifics, at least if encountered on mistletoe plants. Marking of individual birds is, however, necessary to be able to make more definitive statements on this subject.

4.2.5. Post-feeding behaviour of mistletoe-eating birds

A comparison of the sites at which seeds of three mistletoe species were deposited by birds, is given in Table 16. Forty-seven per cent of the seeds of T. natalitius, 42% of the seeds of T. leendertziae and only 17% of the seeds of V. combreticola were carried away from the parent plants. For the Yellowfronted Tinker Barbet alone, the corresponding figures were 61, 50 and 15%, respectively. The number of seeds carried away is inversely related to the duration of the birds' visits (see Section 4.2.3.3) and the retention time of the seed (see Section 4.2.3.4). During long visits, as in V. combreticola, most seeds are regurgitated on the parent plant, and only seeds ingested during the last feeding bout are carried away. A short retention time of seeds results in relatively more seeds being deposited on the parent plant. These two factors, combined, result in a relatively high proportion of seeds of V. combreticola being wasted through deposition on the parent plant or its host. In T. natalitius, however, a high proportion of seeds is carried away from the parent plant, because bird visits were shortest and seeds were retained longest. Only 19% of the seeds were carried away when the pecking method of feeding was used, showing the relative inefficiency of this method for seed dispersal.

Table 16. Number of seeds of three mistletoe species deposited either on the parent plant and its host (H) or on other potential hosts (O), after regurgitation or deposition of the seed during the "pecking method", by birds in the Loskop Dam Nature Reserve

	Mistletoe species					
	T. leendertziae		T. natalitius		V. combreticola	
Bird species	H	O	H	O	H	O
Blackcollared Barbet	9	4	11	-	4	11
Pied Barbet	10	11	-	2	3	-
Yellowfronted Tinker Barbet	100	98	21	33	342	61
Southern Black Tit	13	8	8	-	-	1
Plumcoloured Starling	39	11				
Redheaded Weaver	14	-				
Total	185	132	40	35	349	73

Table 17. Distance (m) of post-feeding flights of birds from plants of three mistletoe species in the Loskop Dam Nature Reserve

	Mistletoe species								
	T. leendertziae			*T. natalitius*			*V. combreticola*		
Bird species	mean	(range)	N	mean	(range)	N	mean	(range)	N
Blackcollared Barbet	35,0	(30-40)	2				36,7	(20-50)	3
Pied Barbet	5,0	(5)	2	15,0	(15)	1			
Yellowfronted Tinker Barbet	19,8	(3-50)	37	24,6	(5->50)[b]	7	34,2	(4-75)	26
Black Tit	4,5	(2-7)	2				20,0	(20)	1
Plumcoloured Starling	68,3	(5->100)[a]	3						

a: >100 m substituted by 150 m
b: > 50 m substituted by 75 m
The difference between the distances of the flights from the three mistletoe species by Yellowfronted Tinker Barbets was not significant ($t_{calc.} = 0,72$, $t_{0,975} = 2,05$; for the comparison between *T. leendertziae* and *V. combreticola*)

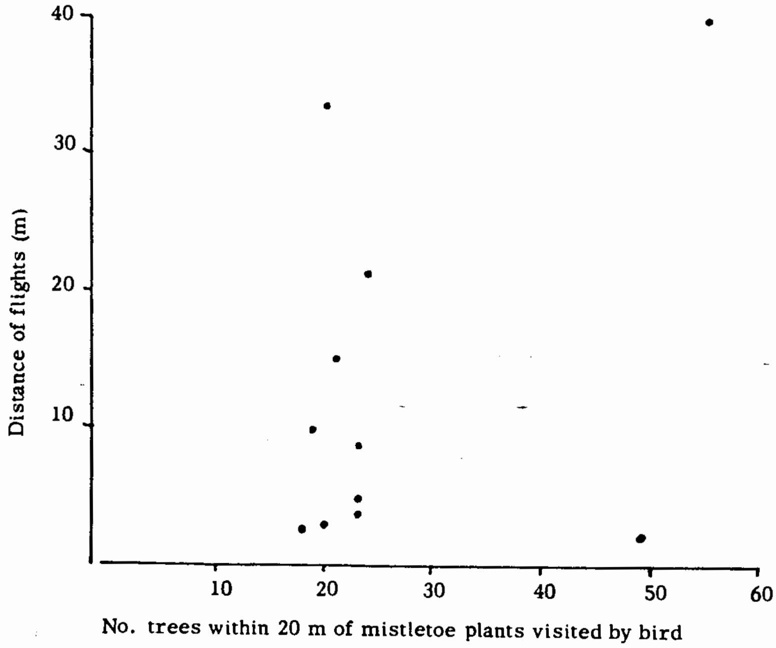


Figure 12. Relation between distance of post-feeding flights of Yellowfronted Tinker Barbets from individual mistletoe plants, and the number of trees within a radius of 20 m of those individuals. Each dot represents the mean distance recorded at each of 11 observation sites

(The function of the regression line derived from these data, is: $f(x) = 0,7833 + 0,0554$. The fitness was, however, very weak ($\chi^2_{calc.} = 116,93$; $\chi^2_{0,05;10} = 3,94$) so that there is apparently no direct relation between the characters represented by the x- and y- axes)

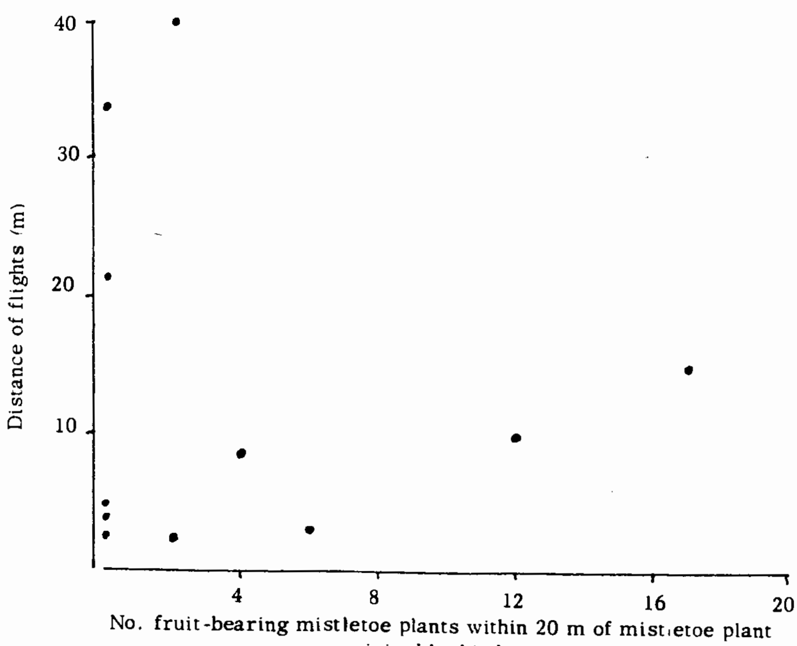


Figure 13. Relation between distance of post-feeding flights of Yellowfronted Tinker Barbets from individual mistletoe plants and the number of fruit-bearing mistletoe plants within a a radius of 20 m from those individuals. Each dot represents the mean distance recorded at each of 11 observation sites

(The function of the regression line derived from these data, is: $f(x) = 9,8717 - 0,4488x$. The fitness was, however, very weak ($\chi^2_{calc.} = 276,89$; $\chi^2_{0,05;10} = 3,94$), so that there is apparently no direct relation between the characters represented by the x and y-axes)

The mean distance of the birds' immediate, post-feeding flights away from mistletoe plants is shown in Table 17. Most flights were shorter than 50 m. Very few exceeded 100 m, with the bird usually disappearing out of view. If the distances of these flights are considered to be good approximations for the distanced at which the seeds, which were consumed last, were deposited (which, in the light of the short retention time, is reasonable), then, seed dispersal apparently occurs not far from the parent plants.

The mean distance of immediate, post-feeding flights by Yellowfronted Tinker Barbets from individual mistletoe plants was plotted against the number of trees within a radius of 20 m (ca. 0,125 ha) of the individual plants (Figure 12), and against the number of mistletoe plants bearing ripe fruit within the same area (Figure 13). No relation was found between the distance of post-feeding flights and either the number of trees or the number of fruit-bearing mistletoe plants in the area around the plant at which the bird had fed. There are several factors which may influence the post-feeding behaviour of birds, including the nutritional state of the bird, the size of its territory (if a territory is held), whether the bird is breeding or not, and the distance to nesting site. In France, Labitte (1952) found that the Mistletoe Thrush Turdus viscivorus was relatively inactive on very cold, cloudy days; sitting for hours near one mistletoe plant. This presumably resulted in many seeds being deposited near the mistletoe plant.

Mousebirds sometimes remained for relatively long periods in a mistletoe plant, resulting in many seeds being deposited near the parent plant. On other occasions, however, they made relatively long post-feeding flights. Tubeuf (1923, quoted by Scharpf & McCartney 1975) found that the maximum distance over which the Mistletoe Thrush (which defaecates mistletoe seeds) actually carried seeds away from the parent plant, was "less than one mile".

4.2.6. Non-mistletoe food of the Yellowfronted Tinker Barbet

All food items observed to be taken by Yellowfronted Tinker Barbets in the field, were recorded. The birds were observed occasionally to hawk insects during October and February - May. Once an individual gleaned an insect from a branch. Apart from the numerous records of feeding on mistletoe fruit, only a few instances of Yellowfronted Tinker Barbets eating other vegetable food were obtained: on 16 June and 25 August an individual was observed eating the rather dry fruit of Rhus leptodictya; on 11 August an individual was observed eating succulent berries of Berchemia zeyheri; on 1 November an individual was observed with an unidentified red fruit in its beak. Once, on 6 August, a tinker barbet was observed feeding on nectar of Aloe castanea. From the bird's behaviour it was obvious that it was sucking nectar from the flower and not searching for insects. During August tinker barbets with orange faces were seen several times, as were also several other species of birds, indicating that they fed on Aloe nectar regularly during that month, particularly in the camp where Aloe species were common. I do not know of any previous reports of Yellowfronted Tinker Barbets feeding on nectar, though Redfronted and Goldenrumped tinker barbets have been reported to feed on nectar of Aloe marlothii in Natal (Oatley 1964; Oatley & Skead 1972).

It is noteworthy that the records of tinker barbets feeding on non-mistletoe vegetable food pertain to June, August and November which fall in the period during which V. combreticola fruit was the only mistletoe fruit available. At this time, feeding pressure on V. combreticola fruit apparently was high, resulting in a relatively low availability of mistletoe fruit (see Sections 4.1.3.1 and 4.2.2).

The scarcity of records of Yellowfronted Tinker Barbets feeding on vegetable food other than mistletoe fruit suggests strongly that this species has a strong preference for (if not dependence on) mistletoe fruit, at least in the study area. This is in agreement with the many reports pointing to this bird's fondness of mistletoe fruit (see Section 2). To my knowledge, there are only two records for the Yellowfronted Tinker Barbet feeding on non-mistletoe fruit: fruit of Rhus pyroides (Anon. 1962) and Ficus (Morse-Jones MS). Thus, Ayres's (1879) report that the Yellowfronted Tinker Barbets which he saw "were almost always on or near a species of mistletoe", is confirmed.

As mentioned, Yellowfronted Tinker Barbets occasionally were observed taking insects. To what extent insects contribute to the species' total diet is, however, not known. Brooke et al. (1972) reported the Yellowfronted Tinker Barbet as a casual termite alate eating species in Rhodesia. In the light of the high lipid content of mistletoe arils (see Section 4.1.6), it seems likely that insect food is taken mainly as a protein-rich food source (e.g. the protein content of some insects, given by Morton (1973) varied between 25-72% on a dry weight basis).

5. SYNTHESIS AND CONCLUSIONS

5.1 Comparison between the seven plant communities with respect to occurrence of mistletoes and mistletoe-eating birds

Short descriptions of the seven plant communities in which the occurence and dispersal of mistletoes were studied are given in section 3.1 .

Observations in the A. caffra - F. saligna community were only possible during March - August 1977. Consequently, the period during which Tapinanthus fruit was available, was over-represented, and the period during which only V. combreticola fruit was available, was under-represented. As the Yellowfronted Tinker Barbet was nearly the sole consumer of V. combreticola fruit, its importance in the A. caffra - F. saligna community would undoubtedly have been much higher than emerges from Table 11, if observations could have been made over a whole year.

The most aberrant plant community in several respects was the C. apiculatum community. This was the only community, of the seven involved, which was situated on north-facing slopes. According to Theron (1 973), the north-facing slopes in the Loskop Dam Nature Reserve are warmer and drier than the plains and the south-facing slopes, resulting in a relatively "harsh" environment. A typical tree of these conditions was Sclerocarya caffra (Theron 1973). Another peculiar feature was that most of the Erianthemum ngamicum plants recorded in the reserve, were found in this community, particularly on S. caffra trees. Erianthemum ngamicum seems to be a species of relatively dry area (e.g. Botswana, where its specific epitheton comes from, and the drier parts of Natal (Frost in litt. 1978; pers. obs.)). The presence of this mistletoe in the C. apiculatum community is thus probably in part a result of relatively dry and warm conditions. Whether the main occurrence of E. ngamicum on S. caffra trees is the result of a real "preference" for S. caffra or the result of the relatively low availability of Acacia trees in the C. apiculatum community, so that S. caffra acts as an alternative host, is not clear. The two possibilities are not mutually exclusive, however, and may act together. The few individuals outside this community grew on Acacia trees, and in Natal I recorded four Acacia species as hosts for E. ngamicum, and in the Kruger National Park it was found only on Ostryoderris stuhlmannii (Van Wyk 1971). This, perhaps, favours the second explanation mentioned above.

The relative scarcity of the three main mistletoe species in the C. apiculatum community may also have been caused partly by the "harsh" conditions, though the relatively low availability of Acacia caffra undoubtedly played a role as well in the incidence of both Tapinanthus species. The "harsh" conditions apparently also influenced the reproductive phenology of the two deciduous Tapinanthus species. The reproductive cycle of T. leendertziae started 3-8 weeks (mean 5,4 weeks) later and ended 0-4 weeks (mean 1,8 weeks) earlier in the C. apiculatum community than in the other communities. In T. natalitius the period between the disappearance of the last fruit and the appearance of the first flower bud was 13 weeks, compared to 1-12 weeks (mean 7,2 weeks) in the other communities. This was caused mainly by the earlier (mean 4,8 weeks) disappearance of its fruit in the C. apiculatum community. The flowers of T. natalitius appeared 0-2 weeks (mean 1,0 weeks) later in the C. apiculatum community than in the other plant communities. This indicates that the "harsh" environmental conditions in the C. apiculatum community had a more pronounced influence on the start of the reproductive cycle in T. leendertziae than in T. natalitius, which is remarkable as flowerbuds of both species appeared in the same period. The influence of the "harsh" conditions at the end of the reproductive cycle was more pronounced in T. natalitius than in T. leendertziae, however. This was most probably the result of the earlier termination (April) of the cycle of T. leendertziae, when environmental conditions were still relatively mild. Towards the end (June) of the cycle of T. natalitius environmental conditions were less favourable, and increasing "harshness" in the C. apiculatum community apparently exerted a more pronounced influence on termination of the cycle than during April. The low number of fruit-eating bird species (Table 9), and of birds in general (pers. obs.) in the C. apiculatum community may also have been partly caused by the "harsh" environmental conditions. The Yellowfronted Tinker Barbet consumed 98% of the mistletoe fruit in this community, the highest proportion of all communities.

The highest production of ripe fruit of T. natalitius was observed in the A. caffra - C. apiculatum community. Tapinanthus leendertziae also produced most ripe fruit in this community as well as in the A. caffra community. The relatively large amount of Tapinanthus fruit attracted a wide variety of birds which ate the fruit, so that the Yellowfronted Tinker Barbet consumed the lowest proportion (of the six communities for which representative data were available) of mistletoe fruit in the A. caffra - C. apiculatum community and the second lowest in the A. caffra community.

The influence of the availability of hosts on the occurrence of mistletoes was obvious in some cases, including the low occurrence of Tapinanthus in the C. apiculatum community. At site 5 in the A. karroo community no Combretum trees were present, and consequently V. combreticola did not occur at that site, whereas it was present at site 4 where both C. apiculatum and C. zeyheri occurred. Relatively few mistletoes occurred in the Burkea community, in which the dominant tree B. africana apparently is not a suitable host for mistletoes. The wide variety of trees in the Camp resulted in an abundant presence of both species of Tapinanthus and both species of Viscum. Viscum rotundifolium occurred in reasonable numbers only in the Camp. A few individuals were found on the lower part of the A. caffra - F. saligna slope, situated just behind the Camp, and they were undoubtedly dispersed to that community by birds from the Camp.

Two bird species, the Green Pigeon and the Cape Robin, were only observed in the Camp, the former being attracted by the large number of Ficus trees. According to Baker (1970) the Cape Robin also occurs in the western part of the reserve, which I did not enter. The Blackcollared Barbet was notably absent from the A. caffra - C. apiculatum community, which was probably caused by the open vegetation as the bird prefers rather well-wooded country (Skead 1950). The individuals observed in the open Burkea communtiy wandered into that community from the Diplorhynchus condylocarpon community on the nearby slope, which was a more closed tree savanna. The Cape and Masked weavers were not observed in the Burkea community and the three communities in the N. E. V., where no permanent water with reeds on the water-side was present. The Redeyed Turtle Dove was apparently also absent from the N. E. V., whereas the Redheadead Weaver was observed only in the N. E. V. within the reserve. The only mistletoe-eating bird species observed in all seven plant communities, were the Yellowfronted Tinker Barbet and the Southern Black Tit. The latter was only observed to eat mistletoe fruit in reasonable amounts in two communities (Table 11), and in three communities it was not observed to eat mistle-toe fruit at all, though the birds were active close to mistletoe plants. This indicates that this species is only an incidental eater of mistletoe fruit. The reasons for the differences in occurrence of fruit-eating birds between the seven plant communities are obvious in some cases, but in others the reasons are not so clear, and undoubtedly occurrence is influenced by many factors.

In conclusion, the Yellowfronted Tinker Barbet was the most important consumer of mistletoe fruit in all plant communities, though in differing degrees. Differences in mistletoe occurrence as well as the timing of the reproductive cycles of the Tapinanthus species were observed. Mistletoe occurrence was mostly influenced by availability of suitable hosts, and possibly by environmental conditions, too, in the case of the C. apiculatum community. The timing of the reproductive cycle of mistletoes did not differ much between the plant communities, except in the C. apiculatum community where the cycles of both Tapinanthus species were shorter than in the other communities. This was probably mainly caused by the relatively warm and dry conditions prevailing on the north-facing slopes on which the C. apiculatum community was situated. Differences in the occurrence of fruit-eating birds between the different plant communities were probably partly caused by difference in the vegetation, presence of nearby water and reeds, and possibly by climatic conditions, too (in the C. apiculatum community), but many other factors are undoubtedly also involved.

5.2 Mutualism between birds and mistletoes

5.2.1 General discussion

Snow (1971) discussed various aspects of fruit-eating by birds, both from the botanical and ornithological points of view, followed by Morton (1973) who discussed advantages and disadvantages of fruit-eating in tropical birds. McKey (1975) apparently was the first scientist to recognize different dispersal strategies in plants whose seeds are dispersed by fruit-eating birds. Howe and Estabrook (1977) extended several aspects of the basic strategies recognized by McKey (1975). Two main patterns of seed dispersal by birds can be discerned: socalled "specialized" fruits dispersed by "specialized" frugivores (model 1 of Howe & Estabrook 1977), and "generalist" fruits dispersed by "opportunistic" or "generalist" fruit-eating birds (model 2). These are, of course, the two extremes of a whole spectrum, many fruits and birds taking intermediate positions in this spectrum.

Model 1 plants usually have germination sites which are predictable in space, so that they need dispersal agents which will effect dispersal of their seeds to such places. They produce relatively large,one-seeded, fruit with a highly nutritious (protein- and fat- rich) pulp or aril, attracting a few specialized birds, which take most of their energetic and nutritive resources from these fruits. The plants produce relatively few fruits over a long period to sustain the small set of dispersal agents. The birds often have specialized feeding habits and/or alimentary tracts.

Model 2 plants, such as colonizing species, usually have germination sites which are unpredictable in space, so that they need a wide variety of dispersal agents with a variety of habits. They produce a pulp consisting mostly of water and carbohydrates to supply water and a quickly available energy source to birds which eat insects for most of their nutritional requirements (protein and lipids). These plants produce much, small-seeded, fruit during a relatively short period to attract these opportunistic fruit-eating birds. The fruiting seasons of congeneric species are often staggered to reduce competition for dispersal agents (e.g., as Snow (1965) found in 19 species of Miconia, in Trinidad).

McKey (1975) suggested that the mistletoes in most respects belong in the group of specialized fruit, with one exception, according to McKey, namely the small size of mistletoe seeds. However, this may be true for the viscoid species, but probably not for all loranthoid species. The seeds of both Tapinanthus species were not small at all, at least not in relation to the main dispersal agent, the small Yellowfronted Tinker Barbet. In this respect it may be important that the main dispersors of mistletoes in the Oriental and Australian regions (the Dicaeidae, see Section 5.4) are also small birds (Mayr & Amadon 1947). The parasitic growing habit of mistletoes poses certain problems not encountered by ground-living plants, particularly during the process of seed dispersal. The most important problem is that seeds have to be deposited on a host branch (a predictable germination site) to be able to produce new plants. All seeds landing on the ground are completely wasted for the plant. Therefore, mistletoes require a reliable set of seed dispersors which plant the seeds on branches in stead of dropping them to the ground.

Mistletoe fruit shows some peculiar features bound up with the special growing habit and its requirements. An energy investment, which is not required in ground-living plants, is the viscin layer whose main function is to attach the seed to a host branch. This layer also protects the seeds from chemical damage in the bird's alimentary tract, and may also help to retain moisture during germination. Furthermore, the seeds are regurgitated by their main dispersor, and also less important dispersors, after a short time, so that possible damage to the seeds is minimized. These factors cause a hard testa, whose main function is to protect the seeds from damage in the alimentary tract, and possibly also from desiccation after dispersal (McKey 1975), to be unnecessary, and it is, indeed, not found in mistletoe seeds. This enhances rapid germination which is necessary for firm attachment of the seeds to its host before it is washed off by rains, knocked off by animals, or becomes detached by weakening of the viscin. The viscin may also serve as a laxative, so as to shorten the time seeds remain in the bird's gut, and thus minimize possible damage. However, this will be important only when the seeds are defaecated (presumably more important in small-seeded Viscum species). The viscin layer also causes the seed to stick to the bird's beak after regurgitation, so that the bird is forced to wipe the seed off, with resulting neat deposition. The larger the seed and the smaller the bird, the more seeds will be wiped off and planted. The viscin layer may serve to provide some food, too (Kuyt 1969), but probably only when the seeds are defaecated, and hence remain longer in the bird's alimentary tract. This may be of importance in the smaller-seeded mistletoes, which have less visible pulp, and which are presumably dispersed by a wider variety of birds, most of which defaecate the seeds.

The Yellowfronted Tinker Barbet is the main dispersor of mistletoe seeds in the Loskop Dam Nature Reserve, and in several respects seems to be ideally suited for this task. The small size of the bird permits it to move easily through the mistletoe plants. It also probably prevents seeds from entering the post-stomach alimentary tract and thus from being defaecated, so that the bird is forced to regurgitate the seeds, and hence to plant them. As the time that the seeds remain in the gut when they are regurgitated is much shorter than when they are defaecated, the rate of handling fruit is increased considerably, so that more food per unit time is consumed, and the damage to the seeds is minimized. The small size of the bird, together with the relatively large size of at least the Tapinanthus seeds, increase the probability that the seed sticks to the bird's beak, so that it is wiped off onto a host branch. The small size of the tinker barbet also results in a relatively small number of fruits taken per feeding bout, resulting in enhanced dispersion of the seeds. The high nutritive quality of the aril presumably enables the tinker barbet to obtain most of its nutritional requirements from mistletoe fruit. Insects (also high quality food) are taken, too, but the extent of this remains unknown. As the amount of time and energy spent on catching insects is presumably higher than when feeding on stationary fruit, high-quality fruit would presumably be preferred to insects.

Larger birds need considerably more fruit per day to obtain their energy requirements than the small tinker barbet. Compared to the 172 fruits of T. leendertziae needed by the tinker barbet per day, a 40 g mousebird would need about 391 fruits per day, a 50 g Blackcollared Barbet 457 fruits per day, and a 65 g Crested Barbet 550 fruits per day (calculated as in Section 4.1.6). To make visits worthwile, the larger birds would presumably have to remain longer on mistletoe plants (as was suggested by field observations, too), and this, combined with the larger number of fruits taken per feeding bout, would result in a higher proportion of the seeds being deposited on the parent plant or its host, or in clusters near each other, which is disadvantageous for the plants because of the wasting of these seeds. It may be that the number of fruit available on plants of at least T. natalitius and V. combreticola is just large enough to attrack the small Yellowfronted Tinker Barbet, but making visits less profitable for the larger frugivores, so that mainly the most efficient dispersor is attracted.

The fruiting seasons of the mistletoes involved in this study were relatively long: 11 weeks in T. leendertziae, 20 weeks in T. natalitius and the whole year in V. combreticola. This provides a continuous supply of mistletoe fruit to sustain a resident tinker barbet population. Because the tinker barbet is the main dispersor of all three species of mistletoes, it would be advantageous that the fruiting seasons be separated as far as possible, which was observed to a large extent in T. leendertziae and T. natalitius.

High quality of seed dispersal(necessary in specialized fruits) is influenced by several factors (McKey 1975; Howe 1977; Howe & Estabrook 1977). Firstly, fruit should be removed as soon as possible after maturation to minimize pre-dispersal predation, low quality dispersal by opportunistic frugivores, and unnecessary investment in the fruit after it has maturated. The rate of removal of fruit after maturation would probably be related to the number of fruit available on a plant at any one time. Where the lowest number of fruit is available (T. natalitius), fruit should be removed soonest, which was, indeed, observed, as few fruit of T. natalitius were allowed to reach the final red stage, and most fruit were eaten while still green (but ripe). Viscum combreticola takes an intermediate position in this respect, whereas T. leendertziae produced fruit in such high numbers at the same time that individual fruits probably remained longer on the plant than in the other two species. However, it was observed, that the rate of removal of fruit was highest in T. leendertziae, so as to correlate with the higher number fruit available. Secondly, the dispersal agent should be reliable, i.e., it should visit the plants regularly throughout the fruiting season. The tinker barbet was the only frugivore observed to eat mistletoe fruit regularly during each month of the year, and is therefore the only reliable dispersor in the study area. Thirdly, the seeds should be voided intact. Regurgitation of the seeds and the short retention time of the seeds (shortest in the Yellowfronted Tinker Barbet), as well as the protection provided by the viscin layer, minimize any possible damage to mistletoe seeds in the bird's alimentary tract, and probably virtually all seeds are voided intact. Fourthly, the seeds should be deposited in a suitable germination site. The regurgitation of seeds ensures that nearly all seeds, handled in this way, are deposited on a host branch, which is the first requirement of a "suitable germination host". Host specifity of the mistletoes, however, also plays an important role, particularly in V. combreticola, and to a lesser extent in T. natalitius. As only one bird species was mainly responsible for the dispersal of the mistletoes with different host specifities, the role of behavioural differences between dispersal agents can be ruled out mostly. It is unlikely that seasonal variation in behaviour should play an important role, particularly as the fruiting seasons of T. natalitius and V. combreticola, which have the most divergent host specifities, overlap completely. Therefore, it seems probable that the fate of the seeds carried to other trees is rather randomly determined. However, as Acacia and Combretum species are abundant, in the study area, and also in the Transvaal generally (Palgrave 1977), this probably does not pose a too large problem for the mistletoes involved. Fifthly, the dispersal agent should depend on mistletoe fruit rather than on other fruit available at the same time. This is definitely the case in the Yellowfronted Tinker Barbet, but in no other bird, at least not in this area. Sixthly, the seeds should be carried away from the parent plant to escape density-dependent mortality. On this point, the quality of

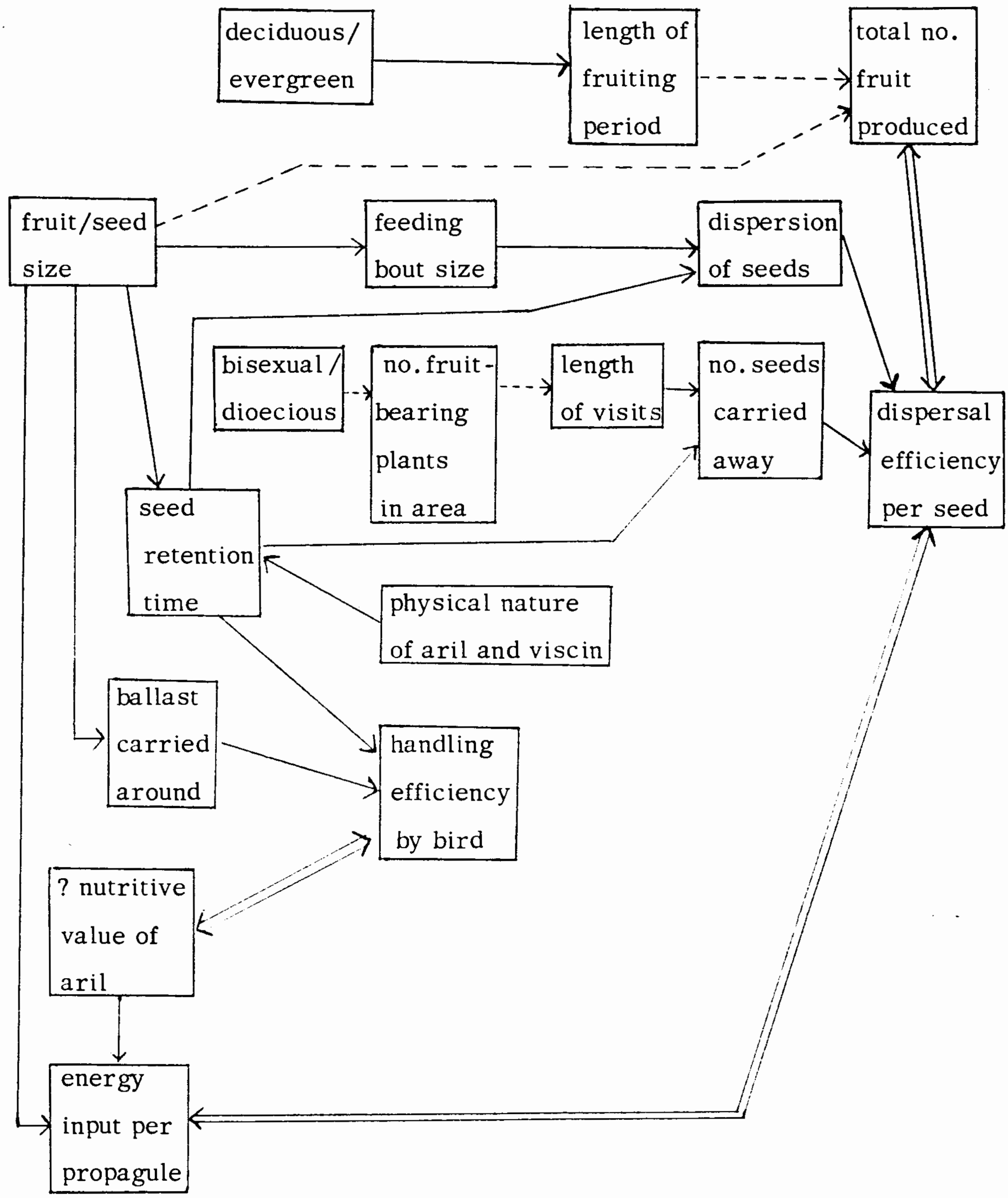


Figure 14. Diagram showing the most important factors and their relationships, involved in the main differences between the dispersal strategies and efficiencies of V. combreticola on the one hand, and T. leendertziae and T. natalitius on the other hand

⟶ causal relationship

- - - -⟶ possible causal relationship

⟺ factors balancing each other

dispersal seems to be hampered, as many seeds are deposited on the parent plant or its host, which is mainly caused by the short retention time of the seeds (and the length of the visits, too, in the case of V. combreticola). The Yellowfronted Tinker Barbet was observed to carry away relatively more seeds of T. leendertziae and T. natalitius than the other birds together, and is thus more effective in this respect. Nevertheless, the relatively high proportion of seeds wasted, in spite of the relatively high fruit quality, is probably the most important price mistletoes have to pay for their special growing-habit, and consequently special dispersal requirements.

The short distance of dispersal of mistletoe seeds, caused mainly by the short retention time of seeds, and probably enhanced by the territorial organization of tinker barbets, presumably results in a slow speed of dispersal. However, as mistletoes require trees as hosts, which presumably spread relatively slowly, mistletoes are not pioneering colonizers, and consequently do not need a high rate of dispersal, so that this disadvantage is possibly not as severe as it looks at first sight. What is needed for successfull reproduction of mistletoes, is that seeds should be deposited preferably on uninfested hosts which as young trees are continuously recruiting in the same area in which the parent plant grows. Direct competition for nutritional requirements between individual mistletoes growing on different individual host trees, even when these hosts are growing within a very short distance of each other, is virtually nihil. For infestation of island habitats (ecological or real islands), however, long-distance dispersal is needed, in which mousebirds may play an important role, because of their habit of defaecating the seeds, as well as the long flights they sometimes undertake. In the case of the smaller-seeded Viscum species, other birds which also defaecate the seeds may also be important for relatively long-distance dispersal.

5.2.2 Differences between the dispersal strategies of mistletoes

Figure 14 shows some of the factors affecting differences between the dispersal strategies of Viscum and Tapinanthus, although the strategies of both are basically similar. An important difference lies in the size of the seeds. The smaller seed of Viscum is correlated with birds taking more fruit per feeding bout and a shorter retention time of the seeds than in Tapinanthus. In Viscum, this results in a more

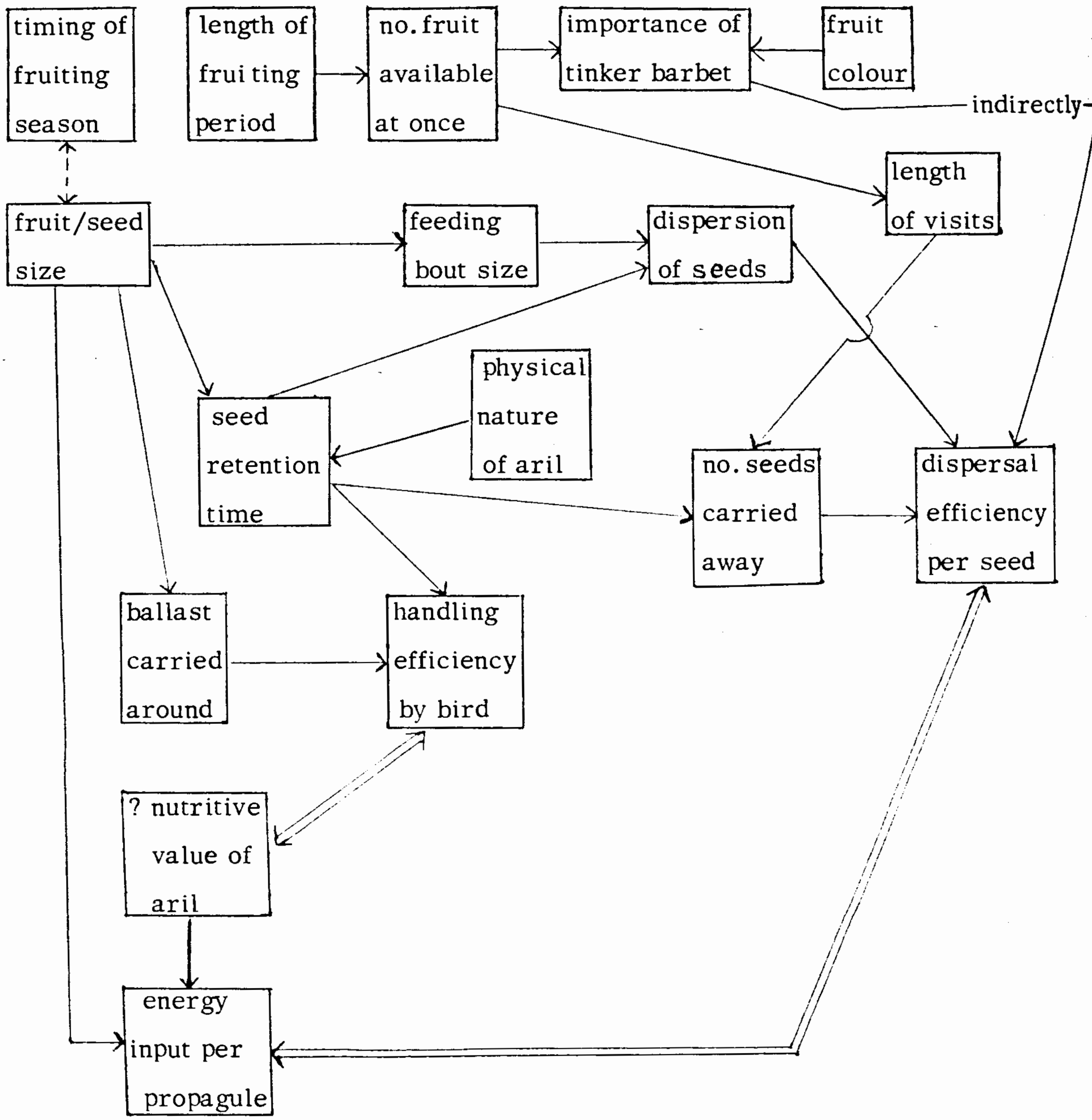
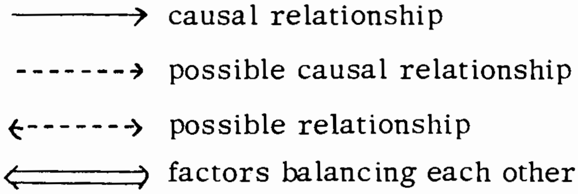


Figure 15. Diagram showing the most important factors and their relationships, involved in the main differences between the dispersal strategies and efficiencies of T. leendertziae and T. natalitius



clustered deposition of the seeds, lowering the dispersal efficiency per seed (i.e., the probability of effective dispersal for each seed). Apart from the smaller size of the Viscum seed, the jelly-like nature of its aril as well as the less-sticky viscin are contributing factors to the shorter retention time of Viscum seeds. The longer visits by birds to Viscum plants, together with the shorter retention time of its seed, result in a relatively small proportion of the seeds being carried away from the parent plant, thereby also lowering the dispersal efficiency per seed. The shorter retention time of Viscum seeds and the lighter mass of the seeds carried around, result in a higher handling efficiency of its fruit by birds, which means that the birds spend relatively small amounts of time and energy per fruit of Viscum. This is, however, counteracted by the presumably lower nutritive value of its aril. The energy input per fruit is lower in Viscum , because of the smaller size of fruit and the presumably lower nutritive value of the aril. Because of the year-round fruit production in Viscum, the total number of fruit produced is much higher than in Tapinanthus.

In conclusion, V. combreticola has a lower dispersal efficiency per seed than Tapinanthus which is, however, compensated for by the higher total number of fruit produced, as well as the lower energy investment in each fruit. Thus, although there are differences in the dispersal efficiency per seed between the species of the two genera, the overall dispersal efficiencies (i.e., the actual number of seeds effectively dispersed in relation to the total amount of energy invested) may be of the same order. A quantification of the various factors and their relationships is, however, a prerequisite for the determination of the dispersal efficiencies of the various mistletoe species.

Figure 15 shows some of the factors affecting differences between the dispersal strategies of T. leendertziae and T. natalitius. The factors involved in the differences are similar to those involved in the differences between Viscum and Tapinanthus, though the differences between the two Tapinanthus species are smaller than those between Tapinanthus and Viscum. Tapinanthus leendertziae has the smaller fruit and seed, and can be regarded in the same light as that for "Viscum" in the preceding discussion. Only those factors and relationships which are different to those already discussed, will be mentioned here.

The larger seed of T. natalitius may be related to the relatively dry season in which its seeds are deposited. Whereas the nature of the viscin is similar in both species, the tougher aril of T. natalitius probably results in a longer retention time of its seeds. Although no precies data are available, it appears as if the aril of T. natalitius is somewhat larger than that of T. leendertziae, and thus presumably contains more nutrients. The low number of fruit available on a plant of T. natalitius at any one time (inter alia related to the extended fruiting period) results in relatively short visits of birds, so that relatively more seeds are carried away. The high number of T. leendertziae fruit available at once, together with the bright red colour of its fruit, attract a wider variety of birds, so that the Yellowfronted Tinker Barbet is less important, which may result in a somewhat lower dispersal efficiency per seed. Whereas the dispersal efficiency per seed appears lower in T. leendertziae than in T. natalitius, the relatively small investment of energy in a fruit of T. leendertziae compensates for the higher loss of its seeds. It may be that the overall number of fruit produced in T. leendertziae is higher than in T. natalitius, but no data are available.

It is clear that the fruits of the three species of mistletoes occupy slightly different positions in the spectrum of dispersal strategies ranging between specialists and generalists. Generally speaking, T. natalitius seems to be farthest on the side of the specialized fruits, V. combreticola more to the generalist-side and T. leendertziae in an intermediate position. However, these relative positions are not quite so easily linear, as the year-round availability of V. combreticola fruit (a specialized character) compared to the seasonal availability of Tapinanthus fruit, shows.

5.2.3 Are mistletoes in Africa entirely dependent on tinker barbets for their dispersal?

In general, this question, which arises naturally from this study, can be answered negatively. Although tinker barbets (Pogoniulus species) are widespread in Africa (a brief account on all Pogoniulus species, their distribution and habitat preference, is given in Appendix 8), they do not occur in a few areas in which mistletoes are found. In southern Africa, these areas are mainly in the region covered by the Orange Free State, the Cape Province west of ca. 25°E and most of Botswana and South West Africa, except for the northern parts (Goodwin & Clancey 1978; McLachlan & Liversidge 1978). Given the presence of suitable host trees mistletoes apparently occur nearly everywhere in Africa south of the Sahara, except probably in areas of extreme desert conditions. In southern Africa there are about 10 loranthoid and about 5 viscoid species occurring entirely or partly outside the range of tinker barbets. These mistletoes are dependent on other birds for their dispersal. Records of mistletoe-eating by birds in areas from which the tinker barbets are absent, include the following: Knysna Loeries eating fruit and rubbing seeds off their beaks, of V. capense, V. obscurum and V. rotundifolium in the Knysna forests (Phillips 1928); Cape Bulbuls eating fruit of V. capense near Port Elizabeth (Liversidge 1972) and Sombre Bulbuls Andropadus importunus eating fruit of the same species on the Cape Peninsula (M. K. Rowan, pers. comm.). No records of birds eating loranthoid fruit in these area are available.

This study showed that birds other than tinker barbets are able to disperse and plant mistletoe seeds. As the Pied Barbet is the only barbet occurring in the western part of southern Africa, it is quite probable that this bird is an important dispersor of loranthoid seeds in the area, though other birds may also be involved. Viscum fruits (particularly those of the small-seeded species) are eaten by a variety of birds. The Pied Barbet is basically similar in morphology to the tinker barbets, except that it is larger and therefore presumably somewhat less efficient as a dispersor of mistletoe seeds. It seems unlikely that there should be major differences in the quality of mistletoe fruit between "tinker barbet areas" and "non-tinker barbet areas", to accomodate for the different dispersors. Larger seeds would presumably adhere more effectively to the larger beak of the Pied Barbet, but no information is available on this subject.

There are strong indication that in areas where tinker barbets occur, they are the normal (and presumably most effective) dispersal agents ofr mistletoe seeds. Room (1972) observed only the Speckled Tinker Barbet eating fruit of T. bangwensis in Ghana. Van Someren (1956) reported that the Goldenrumped and Moustached Green tinker barbets were the chief distributors of seeds of Loranthus and Viscum, in Kenya, whereas Vaughan (1929) found that, in Zanzibar, Loranthus fruit is eaten mainly by the Goldenrumped Tinker Barbet and the Blackeyed Bulbul (this is the only report mentioning a non-tinker barbet bird species as an important mistletoe-eater). Frost (pers. comm.) observed only Goldenrumped and Redfronted tinker barbets eating fruit of E. dregei in the coastal dune forest in Natal, though a wide variety of fruit-eating birds occurred in the forest. My study showed that the Yellowfronted Tinker Barbet consumed more than 80% of mistletoe fruit in the Loskop Dam Nature Reserve.

Therefore, tinker barbets can rightly be called the African "mistletoe-birds" (the main dispersors, the Dicaeidae, of Oriental and Australian mistletoes are called "flowerpeckers" or "mistletoebirds"). It may be that under certain circumstances, certain mistletoe species are entirely dependent on tinker barbets for their dispersal (as seems to be the case with E. dregei in the coastal dune forest at Mtunzini, Natal (Frost, pers. comm.)).

In general, mistletoes are at least dependent on: the availability of suitable host trees; on sunbirds (in the case of loranthoids) or hymenopterids (in the case of viscoids) for pollination; and, on fruit-eating birds for their dispersal. These groups of organisms are therefore limiting biotic factors for mistletoes in Africa.

5.2.4 Are tinker barbets dependent on mistletoe fruit as a main food resource?

The only African species which are reported to be more or less exclusively dependent on mistletoe fruit, are the Yellowfronted and Redfronted tinker barbets (see Section 2). These two species both have wide geographical ranges, but occur mainly in woodland and savanna (Goodwin & Clancey 1978). As mistletoes are light-loving plants, it is likely that they will be found to be more abundant in woodland and savanna than in forest. This might explain why only these two tinker barbets seem to be highly dependent on mistletoe fruit. Although the other tinker barbets which occur mostly in forest habitats (see Appendix 8) are also reported to be fond of mistletoe fruit, it is probable that this food source is of lesser importance to them, because of the relatively low abundance of mistletoes, and the availability of many other fruits, in forests. In this connection, Frost (pers. comm.) has found that the Goldenrumped Tinker Barbet took fruit of many species in addition to those of E. dregei.

Clearly, more field studies on tinker barbets are needed before any definite answer can be given to the question posed above. It would help to look for study areas in which Yellowfronted or Redfronted tinker barbets occur without mistletoes, if such areas exist. Otherwise, it would be fruitfull to see whether these tinker barbets change their diets when mistletoe fruit becomes seasonally unavailable, or whether they migrate to areas in which mistletoe fruit is available.

5.3 The dispersal of mistletoes in a savanna locality (Loskop Dam Nature Reserve) and a coastal dune forest locality (Mtunzini, Natal)

Most of the information reported here was kindly provided by Peter Frost. Also incorporated are observations made by me during a week-long visit in March 1978 to Peter Frost's study area at Mtunzini.

Erianthemum dregei was the only mistletoe species in the forest study area, and it was less common than any mistletoe at Loskop Dam, probably, inter alia, because of the low light-intensity inside the forest, which limits mistletoes mainly to the canopy, as they are light-loving plants. Two reproductive cycles per year occurred in E. dregei, which undoubtedly is permitted mainly by the more even environmental conditions in the forest, whereas T. leendertziae, T. natalitius and E. ngamicum showed only one cycle per year at Loskop Dam where distinct seasonal climatic variations occurred, though the evergreen V. combreticola had a continuous reproductive cycle. The period of ripe fruit availability in E. dregei in the forest was about 14 weeks during each cycle (28 weeks in a year), compared to 11 weeks in T. leendertziae and 20 weeks in T. natalitius at Loskop Dam.

Only the Redfronted and Goldenrumped tinker barbets were observed eating E. dregei fruit in the forest, compared with eight mistletoe-eating birds recorded at Loskop Dam, of which, however, one (the Yellowfronted Tinker Barbet) consumed over 80% of the mistletoe fruit. The Redfronted Tinker Barbet only entered the forest from the surrounding bushveld during winter, and was responsible for 7% of the feeding records. The Goldenrumped Tinker Barbet consumed 93% of the fruit of E. dregei, but it took fruit of many species in addition to those of E. dregei. At Loskop Dam, the Yellowfronted Tinker Barbet was also the most important mistletoe-eater but mistletoe fruit formed apparently the bird's main food resource, permitted among other things by the year-long availability of mistletoe fruit. The relatively low number of fruit available at once, the low conspicuousness of E. dregei plants in the forest, and its lower abundance, may be contributing factors to its restrictedness with respect to dispersal agents.

The number of ripe fruit available on E. dregei plants at any one time was relatively low. As a result of this, and presumably also because of the relatively large population of Goldenrumped Tinker Barbets in the forest, fruit was usually removed at an early stage of maturity: 45% of the fruit taken was green, 34% greenish-red, and 21% red (during the first 2/3 of the fruiting season; later in the season the proportion of green fruit taken dropped). Another feature, not observed in my study, was that overripe red fruit of E. dregei was apparently so soft that the content sometimes would slip out of the fruit when handled, and dropped to the ground (8% of the fruit was lost in this way). Feeding on the firmer green or greenish-red fruit is thus more profitable.

Frost found a definite decline in the rate of removal of mistletoe fruit during the day, which is probably caused mainly by the relatively high tinker barbet population and the relatively low number of mistletoe fruit available at any one time, resulting in a depletion of the fruit resource in the course of the day. Another possible reason, a relatively high intake of insects later in the day to obtain energy-rich food for the night, is less likely because of the high lipid content of the aril of loranthoid fruit (35%, on a dry weight basis, in the aril of T. leendertziae fruit, and the aril of E. dregei fruit seems to be oily, too). At Loskop Dam two feeding peaks were observed, one during the morning and one during the late afternoon.

The seed of E. dregei is smaller than those of both Tapinanthus species at Loskop Dam, with a thin orange aril which is a firm, relatively dry pellicle, more difficult to remove than the aril of both Tapinanthus species. The small size of the seed allows a higher intake per feeding bout. The mean number of fruits taken per feeding bout was 3,9 fruits (1-9; n=50), which is even higher than was found in the Yellowfronted Tinker Barbet feeding on the smaller-seeded fruit of V. combreticola. The period between the swallowing and regurgitation of individual seeds was considerably longer in the Goldenrumped Tinker Barbet (3 min 38 sec; range 2 min - 5 min 25 sec, n=37) than reported for the Yellowfronted Tinker Barbet. It was regularly observed that the Goldenrumped Tinker Barbet regurgitated a seed, and, seeing that the aril had not yet been removed completely, reswallowed it. This behaviour was not observed in the Yellowfronted Tinker Barbet. Apparently, the aril of E. dregei is removed with much more difficulty, which is probably mainly caused by the firmness of the aril, and might also be related to possible differences in stomach structure between the two tinker barbet species (a subject on which, however, no data are available). Seeds of E. dregei were regurgitated, but were often just dropped to the ground, without being planted. Frost found that seeds of green fruit were less sticky than those of fully mature fruit, and it is presumably usually the former that drop to the ground. The small size of the seeds may also contribute to the fact that they do not always stick to the bird's beak, and are dropped easily. Even when the seed is stuck to the bird's beak by a thread of viscin, and the seed is wiped off onto a branch, it is not always firmly attached, and often drops to the ground, too. A relatively high proportion (35%) of the seeds of E. dregei was wasted in this way, whereas Yellowfronted Tinker Barbets neatly planted nearly all mistletoe seeds, including the smaller and less sticky seeds of V. combreticola and probably also V. rotundifolium. Therefore, additional to the size of the seeds, behavioural differences between the two tinker barbet species are probably involved. The Yellowfronted Tinker Barbet always immediately lowered its head characteristically down towards the branch when the seed was being regurgitated, whereas the Goldenrumped Tinker Barbet usually remained upright when regurgitating; it only planted a seed, if the seed was stuck to its beak.

The Goldenrumped Tinker Barbet is a "restless" bird, often leaving quickly after feeding on mistletoe fruit. This may be in part to counteract potentially higher predation, because of the relatively low visibility (due to the lower light intensity and thick vegetation) in the forest. The relatively low numberof fruit available on a plant at any one time, also makes it presumably less profitable to stay at a particular plant for long periods. The relatively high population of Goldenrumped Tinker Barbets in the forest results in more intraspecific encounters, during which the birds usually chased each other. Because other fruit is also freely available and eaten, this may also favour the bird moving on. This restless behaviour, caused by several factors, and the relatively long retention time of the seeds, result in relatively few seeds being deposited on the parent plant itself (6%) and 10% of the seeds were carried away more than 40 m (in a forest edge environment), compared with the relatively high proportion (50 - 85%) of seeds which were deposited on the parent plant or its host by the Yellowfronted Tinker Barbet at Loskop Dam. The very reliable planting of the seeds by the latter species, however, makes up for this.

In conclusion, although the patterns of dispersal of mistletoes in the coastal dune forest and the savanna are basically similar, some interesting differences occur. In the savanna, eight species of birds (of which only one is a tinker barbet) were observed eating mistletoe fruit, whereas in the forest only two species of tinker barbets were recorded to do so. However, for the Yellowfronted Tinker Barbet (the main mistletoe dispersor in the savanna) mistletoe fruit formed probably its main food, whereas the Goldenrumped Tinker Barbet (the main mistletoe dispersor in the forest) takes also fruit of many other kinds (though mistletoe fruit may be relatively important during the period when it is available). These differences between the two biome types are probably to a large extent bound up with the relatively low availability of non-mistletoe fruit in the savanna. The low conspicuousness and less dense dispersion of mistletoe plants in the forest presumably also restrict E. dregei to those species of birds which are able to recognize the plant easily. Apparently the Goldenrumped Tinker Barbet is such a species, and can be regarded as a "mistletoe specialist" (the characteristics of specialist frugivores are discussed in Section 5.2.1). The main differences between the two tinker barbet species involved, are the relatively large proportion of mistletoe seeds dropped to the ground by the Goldenrumped Tinker Barbet, and the longer time they retain mistletoe seeds before regurgitating them, compared to the Yellowfronted Tinker Barbet, which plant nearly all seeds on a host branch.

5.4 Mistletoe dispersal by birds in major biogeographical regions

Palaearctic Region

Over the largest part of Europe, the Mistle Thrush is the most important mistletoe-eating bird (its common name as well as its specific epitheton 'viscivorus were derived from this), though not confined to this food source which is only available during winter and early spring (Tubeuf 1923, quoted by McAtee 1926; Ridley 1930; Labitte 1952; Hardy 1969). The secondmost important species is the Bohemian Waxwing, followed by five Turdus species (Tubeuf 1923, quoted by McAtee 1926; Hardy 1969). In total, Tubeuf (op. cit.) recorded 22 avian species eating mistletoe fruit, including also incidental feeders, and there may be more.

In Sweden, where the Mistle Thrush is relatively uncommon, the Bohemian Waxwing and the Fieldfare T. pilarus are most important (Walldén 1961). In certain areas, where the waxwing is rare, the Blackcap is the most important consumer of mistletoe fruit in France. However, because of its method of dealing with the fruit, this bird does not distribute the seeds far from the parent plant for which the Mistle Thrush is still mostly responsible (Heim de Balsac & Mayaud 1930). Though mistletoe fruit forms only a part of the overall diet of the Mistle Thrush (Ridley 1930), at certain times it can be relatively important for the bird locally. Labitte (1952) found that Mistle Thrushes would remain in certain places in France even during severe winters, if mistletoe fruit was available. The Mistle Thrush, and also the other European Turdus species, are migratory birds. Tubeuf (1923, quoted by McAtee 1926) found some connection between the directions of migrations of these birds, and the distribution of mistletoes in Germany.

Nearly all records of birds eating mistletoe fruit in Europe are for birds feeding on the fruit of the widespread, white-berried, European mistletoe Viscum album. This species is replaced in the eastern Mediterranean by the red-berried V. cruciatum, whose fruit is recorded to be eaten by the Mistle Thrush, the Song Thrush T. philomelos and the Blackbird T. merula (Hardy 1969). Most probably Aristotle, and other commentators of ancient times (see Introduction), referred to this mistletoe being eaten by the Mistle Thrush which he named "ixoboros", translated by Linnaeus into "viscivorus" (Hardy 1969). Fruit of Loranthus europaeus, occurring in central and south-eastern Europe, have been recorded to be eaten by the Mistle and Song thrushes, the Blackbird and the Bohemian Waxwing (Tubeuf 1923, quoted by Ridley 1930; Heim de Balsac & Mayaud 1930).

In most cases the fruit is swallowed whole, and the seeds are defaecated (Heim de Balsac & Mayaud 1930; Wallдén 1961; Borowski 1966) Sometimes seeds stick to the beaks of the birds, before being wiped off (Hardy 1969). Only the Blackcap was recorded to use a method similar to the one used by Southern Black Tits and Redheaded Weavers in South Africa, whereby the fruit is plucked, and deposited on a branch after which both the pulp and the exocarp are removed and eaten (in the South African birds, however, the exocarp is removed before depositing, and discarded, and the seed left behind on the host branch (Heim de Balsac & Mayaud 1930).

An interesting feature, not mentioned for other regions, is the direct predation on seeds of V. album by tits (especially Blue Tits Parus caeruleus), nuthatches (Sittidae) and creepers (Certhiidae), which eat the seeds after they have been deposited on a branch by other birds (Tubeuf 1923, quoted by McAtee 1926; Heim de Balsac & Mayaud 1930; Walldén 1961). It is remarkable that in Europe tits are recorded to eat the seeds, whereas I observed Southern Black Tits eating the pulp and planting the seeds of mistletoes.

In conclusion, the most important mistletoe-eating bird-species in the Palaearctic Region is the Mistle Thrush, which consumes, however, much other fruit, too (even when mistletoe fruit is available), and thus cannot be regarded as a typical "mistletoe specialist." (Interestingly, whereas Dement'ev and Gladkov (1968) record mistletoe fruit in the diet of the Bohemian Waxwing in the Sovjet Union, they do not mention it for the Mistle Thrush.)

Nearctic Region

Martin et al. (1951) listed 13 species of birds known to eat mistletoe fruit, of which the Phainopepla and the Cedar Waxwing Bombycilla cedrorum (see also Scharpf & McCartney 1975) are most important, followed by the Western Bluebird Sialia mexicana (see also Ridley 1930; Cowles 1936; Miller & Stebbins 1964). The waxwing is widespread over the whole of the United States, but the Phainopepla only occurs in the south-western border states from Texas to California, and farther south in Mexico (Crouch 1943; Martin et al. 1951). As the habitat in which the Phainopepla and the Cedar Waxwing occur, are completely different (Martin et al. 1951), competition for mistletoe fruit between them in the areas where they are sympatric, is likely to be minimal.

It is difficult to find accounts of the Phainopepla in the literature which do not mention its close relationship to mistletoes (Grinnell 1914; Crouch 1943; Van Tyne & Berger 1961; Miller & Stebbins 1964). In winter and early spring (when mistletoe fruit is available) the Phainopepla's distribution seems to be bound up nearly completely with the occurrence of mistletoes (Crouch 1943). Walsberg (1975a) studied this bird in detail in California, and found that it was territorial around patches of mesquite supporting mistletoe in the desert during the first nesting cycle. After the first nesting cycle (when mistletoe fruit was no longer available) the birds migrated to the coastal woodlands where they nested a second time, feeding mostly on Rhamnus crocea berries, during which no feeding territories were held (Walsberg 1975a).

As in the Palaearctic Region, mistletoe fruit is swallowed whole, after which the seeds are defaecated, at least in the Phainopepla (Walsberg 1975b) and the Cedar Waxwing (Sutton 1951).

In conclusion, over most of the Nearctic Region the Cedar Waxwing is the most important mistletoe-eating bird (though not confined to this food (Martin et al. 1951)), but in the arid extreme south-western area the Phainopepla is most important, and in winter, seems to be restricted mostly by the occurrence of mistletoes. Because of its nearly complete dependence on mistletoe fruit in the arid and desert regions in winter, the Phainopepla can be regarded as a relatively specialized (though seasonal) mistletoe-eating bird, though no major morphological (Walsberg 1975b) or behavioural adaptations seem to occur. It is the most northerly occurring species of the typical Middle-American family Ptilogonatidae (Van Tyne & Berger 1961), of which other species are also recorded to eat mistletoe fruit (see under Neotropical Region).

Neotropical Region

Few records for the South American continent itself are available, but quite a lot of information on Central America and its islands is available, which is probably largely a reflection of the distribution of ornithological research in the neotropics.

Reiche (1904, quoted by Docters van Leeuwen 1954) recorded the Chilean Mockingbird Mimus thenca (largely insectivorous (Meyer de Schauensee 1971)), as eating fruit of the mistletoe Phrygilanthus aphyllus in Chile. Van Tyne and Berger (1961) referred to a South American tyrant flycatcher Phaeomyias as eating mistletoe fruit, whereas Meyer de Schauensee (1971) states that euphonias (genus Euphonia of the family Thraupidae) "subsist mainly on mistletoe berries", which is also reported from the West Indies, where they among other names are called "mistletoe birds" (Wetmore 1914; Bond 1960), and Central America (Robin & Heed 1951; Sutton 1951; Slud 1964). The Gray Silky Flycatcher P. caudatus is reported to eat mistletoe fruit in Costa Rica (Skutch 1965). Snow and Snow (1971), in a study on the feeding ecology of tanagers (Thraupidae) and honeycreepers (Coerebidae) in Trinidad, found mistletoe fruit to be a relatively important part (14%) of the food of the Violaceous Euphonia E. violacea, whereas they recorded seven other species (not euphonias) to take mistletoe fruit, too. Leck (1971, 1972) found at least 15 species of birds feeding on the small fruit of the mistletoe Oryctanthus occidentalis in Panama, including five tyrant flycatchers (Tyrannidae), five tanagers, two vireos (Vireonidae), one pigeon (Columbidae), one seedeater (Emberizidae) and one manakin (Pipridae). It formed a relatively important part of the diet of most tanagers and tyrant flycatchers. Gosse (1847, quoted by Ridley 1930) recorded the Redeyed Vireo to regurgitate a seed of Phoradendron, in Jamaica,and that the Solitaire Bird Myadestes armillaris also fed on mistletoe fruit. Two records are available for the islands west of South America. Skottsberg (1928, quoted by Ridley 1930) recorded Turdus magellanicus to eat fruit of Phrygilanthus. Gifford (1919) observed the Smallbilled Tree Finch Camarhynchus pauper feeding on mistletoe fruit at the Galapagos islands, to which Ridley (1930) added that "it seems probable that the seeds of the latter plant was introduced to the islands by this bird".

Leck(1972) reported that the tanagers feeding on mistletoe fruit "peeled the edible pericarp and dropped the seed", so that they are presumably not very efficient dispersors; the tyrant flycatchers swallowed the fruit whole, and regurgitated the seed (Leck 1972), which was also recorded for the Redeyed Vireo (Gosse op. cit.). The silky flycatchers and the euphonias (apparently the most important mistletoe dispersors in the Neotropical Region) are reported to swallow the fruit whole and to defaecate the seeds (Sutton 1951).

The preference for mistletoe fruit in euphonias can be related to the specialized digestive tract found in members of this genus (and in Chlorophonia viridis), but not in the other genera of the Thraupidae (Forbes 1880; Wetmore 1914; Steinbacher 1935). No muscular gizzard occurs. The part between the glandular proventriculus and the duodenum is thin-walled, extensible and non-glandular, and no cardiac or pyloric constrictions are present. This organization of the alimentary tract in birds which feed almost exclusively on mistletoe fruit, allows a relatively large number of relatively large fruits to be taken in one feeding bout, and a rapid passage of the seeds through the gut (a subject for which, however, no quantitative data are available). The plant probably benefits through the absence of a muscular gizzard in the bird, since the seeds (which are rather vulnerable because of the absence of a testa) pass undamages, while the nutritional elements are still removed.

In conclusion, although a number of avian species are reported to eat mistletoe fruit in the Neotropical Region, there is one group, the small euphonias, which subsist mainly on mistletoe fruit, and which have an alimentary tract ideally suited for this diet, and they can therefore be regarded as "mistletoe-specialists". The silky flycatchers are probably also important mistletoe-eaters in some areas (cf. Phainopepla nitens in the south-western United States).

Oriental Region

This region is characterized by the presence of a specialized group of small mistletoe-eating birds, the flowerpeckers (or mistletoe birds) of the genus Dicaeum. Apart from two incidental records for leafbirds (Irenidae), all other records of mistletoe-eating are for Dicaeum species. Koorders (1909) recorded loranthoid fruit from a stomach of a Bluewinged Leafbird Chloropsis cochinchinensis in Java, and Keeble (1896) once shot an individual of C. jerdoni in Ceylon with whole fruit of Loranthus loniceroides in its stomach.

Nearly every report on a Dicaeum species mentions its relationship with mistletoes, and the birds seem to feed exclusively on these fruit, when they are available, throughout the Oriental Region: India (Ali 1931, 1936; Ali & Abdulali 1938), Ceylon (Keeble 1896), South China (Caldwell & Caldwell 1931), Malaysia (Delacour 1947), the Philippines (Delacour & Mayr 1946) and Indonesia (Docters van Leeuwen 1954). This relationship is the more remarkable as flowerpeckers also feed extensively on the nectar of loranthoid flowers, and are important pollinators of loranthoid species, though not exclusively so (Mayr & Amadon 1947; Docters van Leeuwen 1954). They have tongues adapted for nectar-feeding similar to sunbirds, though variations occur within the genus (Mayr & Amadon 1947). Insects are taken, too, by these birds. The alimentary tract of several Dicaeum species (first described by Cammerloher 1928, quoted by Docters van Leeuwen 1954; and first illustrated by Dammerman 1929) shows a remarkable deviation from the "general type" not recorded for any other group of birds (Desselberger 1931; Mayr & Amadon 1947; Docters van Leeuwen 1954). The muscular gizzard is a blind sac with a sphincter at its opening. When insect food is taken, it enters the gizzard where it is ground down. When mistletoe fruit is taken, however, the sphincter is apparently contracted and the gizzard-opening is closed, so that the fruit is shunted directly from the oesophagus to the intestine. In this way, insects can be taken and ground, whereas mistletoe seeds, which do not need grinding, can pass unharmed and rapidly, sometimes within 5-10 min (Ali 1931; Docters van Leeuwen 1954), through the alimentary canal.

Some flowerpeckers, such as D. agile, seem to swallow only the "fleshy pericarp" and to wipe the seeds on a branch (Ali 1931), which is, however, somewhat doubted by Docters van Leeuwen (1954). Most flowerpeckers, swallow the seed and drop the "skin". Van Heurn (1922, quoted by Docters van Leeuwen 1954) described a remarkable behaviour during defaecation in flowerpeckers: "when defaecating, the bird suddenly sags visibly in the heels and simultaneously shifts its position with astonishing agility along the twig covering a distance of 20-30 cm while its body rocks horizontally to and fro and this rapidly". By this behaviour the bird ensures that the seed is glued to the branch, and does not remain stuck to the vent feathers (which could happen easily because of the stickyness of the seed, as well as the small size of the bird), and the seeds are, thus, not dropped to the ground. This behaviour was observed regularly by Docters van Leeuwen (1954), too, and he found that nearly all mistletoe seeds were effectively glued to a branch in this way.

In conclusion, the dispersal of mistletoes in the Oriental Region seems to be carried out nearly entirely by the small flowerpeckers which live in a double relationship with mistletoes by pollinating the flowers and eating the fruit. Both the structure and function of the alimentary tract, as well as the birds' behaviour during defaecation of mistletoe seeds, are closely related to the dispersal of mistletoes.

Australian Region

Although various species of birds are recorded to eat mistletoe fruit in Australia (Blakely (1922) recorded 22 species), one bird is consistently referred to as a dispersor of mistletoe: the Swallow Mistletoebird (Ramsay 1886; Ashworth 1896; Lawrence & Littlejohns 1916; Heumann 1926; Keast 1958; Kenneally 1973). This species is the only member of the flowerpecker family occuring in Australia (Mayr & Amadon 1947). Though other fruit is taken, too, mistletoe fruit forms its staple food when available, and it seems to be essential as food for nestlings (Lawrence & Littlejohns 1916). The migrations of this bird within Australia as well as the timing of its breeding season in various parts of the continent seem to be linked to the availability of mistletoe fruit (Keast 1958). There are a few areas where the bird is uncommon and where the dispersal of mistletoes is effected mainly by the Australian Silvereye (Johncock 1902, 1903; Keast 1958) and other species (Brittlebank 1908; May 1941). Dicaeum hirundinaceum is not important as pollinator of mistletoe flowers (Keast 1958), as is the case in its Oriental congenerics.

"Polynesian Region"

No records of birds feeding on mistletoe fruit in the Polynesian islands are available. One species of mistletoe, Korthalsella articulatum (a viscoid species), is widespread in these islands (Guppy 1906; Carlquist 1967), but other species also occur (Guppy 1906). According to Carlquist (op. cit.), the dispersal of mistletoes to and between these islands probably occurred mostly by means of endozoochory, i.e., the seeds being carried internally and defaecated by animals.

Conclusions

Certain interesting facts emerge from the foregoing account. A number of birds take mistletoe fruit in the predominantly temperate regions (Palaearctic and Nearctic), but no one species depends mainly on mistletoe fruit, though mistletoe fruit may be relatively important for some species (waxwings, Mistle Thrush) during particular periods under particular circumstances. The Phainopepla, which is heavily dependent on mistletoe fruit during the winter, is probably best considered to be a central-American element, as it occurs in the extreme south-west of the United States and in Mexico, and the other members of its family are typically central-American in distribution.

In each of the tropical regions there exists a group of mistletoe specialists. Mistletoe fruit is an important part of their diet, and they are the main dispersors of mistletoe seeds. All members of these groups are typically small birds.

In the Oriental-Australian area the members of the genus Dicaeum are the typical "mistletoe birds". These birds seem to be nearly the sole dispersors of mistletoe seeds, particularly in the Oriental Region. Furthermore they feed on both nectar and fruit of mistletoes, and in this habit they differ from the other groups of mistletoe dispersors. Their tongues are adapted for feeding on nectar, and their alimentary tracts and behaviour during defaecation, are highly adapted for feeding on mistletoe fruit.

In the Afrotropical Region, the tinker barbets are the most important mistletoe dispersors. They differ from mistletoe-dispersing birds in the Neotropical and Australo-Oriental regions in that they do not defaecate mistletoe seeds, but regurgitate them, to which their "seed planting" behaviour is related. In the light of this, it is not surprising to find that the tinker barbets do not have a highly specialized alimentary canal adaptively organized along lines found in the flowerpeckers and euphonias. Indeed, the structure of the stomach of the Yellowfronted Tinker Barbet does not differ substantially from that found in the Blackcollared and Pied barbets. However, in all three species the stomach is relatively thin-walled compared to that of the Crested Barbet (Godschalk 1976). It is noteworthy that, whereas species of barbets (though fewer species, and relatively unrelated to African barbets, and larger than tinker barbets) occur in the Neotropical and Oriental regions (Van Tyne & Berger 1961), I was not able to find any record of mistletoe-feeding by these extra-African barbets.

In the Neotropical Region euphonias are described as mistletoe specialists. Their alimentary tract is adapted to their diet, but in a completely different way to what is found in the flowerpeckers. This can be related to the nearly complete absence of insects in the diet of euphonias and, thus the absence of the need for a muscular gizzard. The flowerpeckers and the tinker barbets take insects. According to Skud (1964), the White-vented E. minuta and Scrub euphonias E. affinis have "the pronounced habit of sidling along branches and exaggeratedly shifting or stretching (their) tail from side to side", which he apparently observed regularly. He did not mention whether this behaviour was exhibited during defaecation, or not, but it is remarkably similar to the behaviour associated with defaecation in the flowerpeckers. The small size of the bird, and the highly viscous nature of mistletoe seeds might promote their adhension to the bird's vent feathers, causing it to " wipe " its tail onto the branch.

Finally, whereas in each major tropical region of the world a particular group of avian species is specialized for a diet based primarily on mistletoes, each group has its own peculiar set of behavioural and anatomical adaptations for feeding efficiently on the products of mistletoes. Although the basic framework of the inter-relationships between mistletoes and their major avian dispersors in the different regions is now known, much more detailed information covering both botanical and zoological elements is needed to improve our understanding of the optimal arrangements of exchanges and processes in what appear to be highly co-evolved natural systems.

5.5 Postscript

This study was concerned mainly with three species of mistletoes in one study area. In order to obtain a more complete picture of the relationships between mistletoes and fruit-eating birds in Africa, more detailed studies are needed. Such studies should be carried out on as many different mistletoes as possible, in a wide range of habitats and climatic regions. Areas should be included which do not contain tinker barbets (e.g., western Southern Africa), and also areas in which Pogoniulus species other than P. chrysoconus occur. In southern Africa these include: P. pusillus (Natal, eastern Cape); P. bilineatus (coastal strip Natal, detailed data on this species are currently being collected by P. G. H. Frost); P. olivaceus (Ngoye Forest, Natal); and P. simplex (Mozambique). These birds should be studied in different vegetation types, if possible. The feeding ecology of tinker barbets, including in areas where no mistletoes occur (if such areas exist), is also an important field for investigation.

Additional to those ornithological aspects which are covered in this study, attention in future needs to be given to the social organization of the main dispersors. Also a detailed comparative study of the anatomy of the alimentary tracts of tinker barbets, other barbets and frugivores in general is needed. Much more detailed experimental work with wild-captured birds is needed to obtain data on the exact way different birds deal with different mistletoe fruits, as well as the time mistletoe seeds are retained. Other local, indigenous fruit should also be fed to the captive birds to compare the methods used by the birds in dealing with mistletoe seeds, and the retention times of mistletoe seeds compared with seeds of other plants. The birds' preferences for different kinds of fruit in relation to mistletoe fruit need to be investigated. More data on the exact fate of mistletoe seeds after being eaten and egested, should be collected, too.

Future studies should also include small-seeded, thin-exocarped Viscum species, because they probably differ in their dispersal strategies from larger-seeded, thick-exocarped Viscum species. Data on fruit size and anatomy, aril quality, the number of fruit produced and reproductive phenology should be collected, and related to the hosts on which the mistletoes grow, as well as the habitats in which they grow. Observations could be made at large and small plants of the same species, to establish whether there are differences in the rates at which birds visit the plants, and in the "dispersal success" of plants of different sizes. The fruiting phenology of other local, indigenous plants should be monitored, as well as the feeding ecology of mistletoe-eating birds feeding on these fruit, to establish the degree of interspecific competition for dispersal agents between mistletoes and other fruit-bearing plants, as well as the degree of the dependence of various frugivores on mistletoe fruit. In general, the different factors and processes involved in the dispersal strategies of mistletoes, both from the ornithological and botanical viewpoints, need to be more precisely described and quantified. I hope that my study will serve as an impetus for further research to unravel the intricate inter-relationships between mistletoes and fruit-eating birds in Africa.

6. SUMMARIES

6.1 English summary

1. The structures of the fruits of the three species of mistletoes were basically similar : a "seed", a sticky viscin layer (for attachment to a host), an aril (to attract avian dispersors) and an exocarp. The nature of the aril differed between Tapinanthus and Viscum mistletoes.

2. Tapinanthus leendertziae had a wide variety of host species, whereas T. natalitius occurred mainly on mimosoid hosts. The most important host species for these two mistletoes was Acacia caffra, because of its abundance. Viscum combreticola was virtually restricted to Combretum hosts.

3. Tapinanthus leendertziae produced many fruits simultaneously during a relatively short period (11 weeks), whereas T. natalitius produced fewer fruits at any one time, but continued to produce fruit over a more extended period (20 weeks). The flowering and fruiting peaks of both Tapinanthus species were separate to a large extent, resulting in relatively low competition for pollinators and dispersors. Viscum combreticola produced flowers and fruit throughout the year, and carried moderate amounts of fruit at any one time.

4. Viscum flowers were insect-pollinated. Tapinanthus flowers were bird-pollinated, by Whitebellied and Black sunbirds in my study area. The two Tapinanthus species differed in the way their flowers opened. No fruit was formed in T. natalitius and very little fruit was formed in T. leendertziae when their flowers were made inaccessible to birds.

5. Germination of mistletoes was not enhanced by passage of their seeds through the

alimentary tracts of birds.

6. The aril of T. leendertziae fruit had relatively high protein (9%) and lipid (35%) contents, and consequently a high energy content, which make this fruit a good food resource for birds. The amino acid composition of the aril of T. leendertziae fruit showed some major differences compared to whole fruit of Loranthus europaeus, mainly a lower proline and higher leucine and valine contents.

7. The Yellowfronted Tinker Barbet was the most important mistletoe-eater (64% of T. leendertziae fruit, 80% of T. natalitius fruit and 94% of V. combreticola fruit). Seven other species of birds were observed eating mistletoe fruit. Tapinanthus leendertziae had the widest variety of potential dispersors and V. combreticola the lowest, which could be related partly to the quantity and quality of fruit produced.

8. The rate of removal of fruit was highest in T. leendertziae (2,1 fruits/h), lower in V. combreticola (1,2 fruits/h) and lowest in T. natalitius (0,4 fruits/h), which can mainly be related to the number of fruits available at one particular time in the different species. The rate of removal of V. combreticola fruit was higher (1,6 fruits/h) during the months when no Tapinanthus fruits were available, than during the period when Tapinanthus fruits were available (0,6 fruits/h). In T. leendertziae two feeding peaks could be discerned; in the morning (minor peak) and late afternoon (major peak), probably the result of avoidance of heat stress by the birds. Fruit of T. natalitius was taken at a steady rate throughout the day. During spring and summer the pattern in V. combreticola was similar to that found in T. leendertziae, probably for the same reason, but in winter most fruit was taken between 10h00 and 16h00, presumably because heat stress played a less important role and the days were shorter.

9. Three methods of dealing with mistletoe fruit were observed. In the most frequently observed (and most effective) method, used by the most important mistletoe dispersors, the seed is regurgitated shortly after being swallowed, and subsequently wiped off onto a host branch. Mousebirds defaecate the seeds, during which many seeds are wasted on the ground, but this method may be relatively important for long-distance dispersal because of the relatively long retention time of the seeds. Southern Black Tits and Redheaded Weavers did not swallow seeds, but planted them directly on a nearby branch and ate parts of the aril. The seeds were usually planted on or very close to the parent plant by these two species.

10. Fruits of T. leendertziae and V. combreticola were usually taken when red, but those of T. natalitius usually when still green or greenish-yellow, probably because of the relatively low numbers of fruit available at any one time in the latter species.

11. The number of fruits taken per feeding bout by the tinker barbet was 1,6 for T. natalitius, 1,9 for T. leendertziae and 3,2 for V. combreticola, and is thus inversely related to the size of the seeds. In other birds the same pattern was observed, but the actual numbers of fruits were higher, because of the larger size of those birds.

12. The "handling time" for mistletoe fruit was lowest in the tinker barbet. The time spent per fruit (from swallowing to regurgitation of the seed) was related to the size of the seeds: about 60 sec for T. natalitius, about 37 sec for T. leendertziae and about 30 sec for V. combreticola. The number of fruits taken per feeding bout did not influence the overall number of fruits handled per unit time.

13. The only aggressive encounters between birds feeding on mistletoe fruit were observed between Yellowfronted Tinker Barbets, which often chased each other violently, indicating that they held mutually exclusive territoriums.

14. A high proportion of mistletoe seeds was deposited on the parent plant or its host (53% for T. natalitius, 58% for T. leendertziae and 83% for V. combreticola), mainly caused by the short retention time of the seeds by the birds, and it was directly related to the duration of visits to different mistletoes. No relation was found between the distance of the post-feeding flights by Yellowfronted Tinker Barbets from the mistletoe plants on which they had been feeding, and the number of trees or the number of fruit-bearing mistletoe plants around the host tree.

15. The Yellowfronted Tinker Barbet was observed on only three occasions to take non-mistletoe fruit, and during August the birds fed on nectar. Insects were taken, too. The tinker barbet's main food resource is mistletoe fruit.

16. Differences were found between different plant communities with respect to the occurrence of fruit-eating birds and mistletoes. The C. apiculatum community was most aberrant, probably mainly caused by the relatively dry and warm conditions prevailing in that community. Both Tapinanthus species had relatively short reproductive periods in this community.

17. A close interrelationship existed between mistletoes and the Yellowfronted Tinker Barbet in the Loskop Dam Nature Reserve; the tinker barbet being the most

important and efficient dispersor of mistletoe seeds, and the mistletoes providing the tinker barbet with most of its food, in the form of a highly nutritious aril. The regurgitation method is the most efficient way for depositing the seeds neatly and unharmed on a host branch, but resulted in a relatively high proportion of theseeds being deposited on the parent plant or its host, and therefore effectively wasted. For long-distance dispersal, the defaecation method is probably more important.

18. Differences in dispersal strategies were observed between the three common mistletoe species, mainly promoted by the size of the seed , the nature of the aril, the fruiting season, the number of fruits available simultaneously, and possibly the nutritious quality of the aril. Tapinanthus natalitius seems to have the highest "dispersal efficiency" per seed but presumably produces the lowest quantity of fruit. Viscum combreticola has the lowest "dispersal efficiency" per seed, but produces definitely the highest numbers of fruit.

19. Tinker barbets are the main dispersors of mistletoes all over Africa, except in a few areas (mainly western southern Africa) where they do not occur, and where, consequently, other species are responsible for the dispersal of mistletoes.

20. The savanna-inhabiting tinker barbet species seem to be more dependent on mistletoe fruit than the forest-dwelling species, though probably all tinker barbets prefer mistletoe fruit when it is available.

21. Though the basic patterns of dispersal of mistletoes were similar in the savanna at Loskop Dam and the coastal dune forest in Natal, there are some relative differences, of which the most important ones are that Goldenrumped Tinker Barbets (the main dispersor in the forest) also eat much other fruit (but probably prefer mistletoe fruit when it is available). In the forest, mistletoe fruit was only taken by tinker barbets. Furthermore, they drop 35% of the seeds to the ground, and they retain seeds longer than Yellowfronted Tinker Barbets.

22. In the temperate biogeographical regions, a wide variety of birds take mistletoe fruit, although some birds are more important as dispersors than other, but none of them show special adaptations for this diet. In each of the three tropical regions a group of "mistletoe specialists " occur, exhibiting adaptations, for this diet, and which are to a relatively large extent dependent on mistletoe fruit, at least when it is available.

23. In the Oriental/Australian regions the flowerpeckers Dicaeum are the "mistletoe

specialists", both pollinating (though not exclusively so) and dispersing mistletoes. Their muscular gizzard is a blind sac which only receives insect food, and mistletoe seeds pass directly to the intestine, so that the retention time of seeds is short (often <10 min). Their behaviour during defaecation ensures that most of the seeds are glued to a branch.

24. In the Afrotropical Region the tinker barbets (Pogoniulus) are the main dispersors of mistletoe seeds, and their habit of regurgitating, and subsequently wiping off the seeds onto a branch, is highly effective in dispersing and planting mistletoe seeds.

25. In the Neotropical Region the euphonias (Euphonia) subsist mainly on mistletoe fruit and are the main dispersors. They do not have a muscular gizzard, and their alimentary tract is "just a tube", with an extendible portion between the proventriculus and the duodenum, facilitating the rapid and unharmed passage of mistletoe seeds.

6.2 Afrikaanse opsomming

1. Die struktuur van die vrugte van die drie bestudeerde voëlentsoorte was basies dieselfde nl. 'n "saad", 'n klewerige viscinlaag (vir vashegting aan 'n gasheertak), 'n arillus (vir aanlokking van voëls wat die sade versprei), en 'n eksokarp. Die aard van die arillus was verskillend in Tapinanthus en Viscum.

2. Tapinanthus leendertziae het 'n wye verskeidenheid gasheerspesies gehad, terwyl T. natalitius grotendeels beperk was tot mimosoïede spesies. Die belangrikste gasheer vir hierdie twee spesies was Acacia caffra vanweë sy talryke voorkoms. Viscum combreticola het byna net op Combretum-spesies voorgekom.

3. Die verskillende fenologiese stadiums is dwarsdeur die jaar geproduseer in V. combreticola, maar seisoengebonde in beide Tapinanthus spesies. Viscum combreticola het 'n middelmatige getal vrugte op enige tydstip beskikbaar gehad. Tapinanthus leendertziae het 'n groot getal vrugte binne 'n betreklike kort tyd (11 weke) geproduseer, en T. natalitius het 'n klein getal ryp vrugte tegelykertyd beskikbaar gehad, maar oor 'n langer tydperk (20 weke). Die blom- en vrugpieke van die twee Tapinanthus spesies was tot 'n groot mate geskei, wat 'n verminderde kompetisie vir bestuiwers en verspreiders tot gevolg gehad het.

4. Viscum blomme word vermoedelik hoofsaaklik deur hymenopteride insekte bestuif,

terwyl Tapinanthus blomme deur suikerbekkies bestuif word, in die studiegebied deur die Witbors- en Swart suikerbekkies. Die manier van blom-opening was verskillend in die twee Tapinanthus spesies. In T. natalitius is geen vrugte gevorm wanneer voëls van die blomme weggehou is, en in T. leendertziae het slegs 'n baie klein deel van die blomme vrugte gevorm onder sulke omstandighede. Hierdie verskil kan waarskynlik toegeskryf word aan die verskil in die blom-openingsproses.

5. Die deurgang van voëlentsade deur die spysverteringstelsel van voëls het nie ontkieming aangehelp nie.

6. Die arillus (wat die verspreider aanlok) van die vrug van T. leendertziae het 'n hoë proteïen (9%) en vetinhoud (35%), en gevolglik 'n hoë energieinhoud, wat hierdie vrugte 'n goeie voedselbron maak vir sowel energie as proteïenboumateriaal. Die aminosuursamestelling van die arillus toon enkele opmerklike verskille met heel vrugte van Loranthus europaeus, hoofsaaklik 'n laer prolien- en 'n hoër leusien- en valieninhoud.

7. Die Geelkoptinker (Pogoniulus chrysoconus) was die belangrikste voëlentvreter (64% van die vrugte van T. leendertziae, 80% van T. natalitius en 94% van V. combreticola), wat gedeeltelik toe te skryf is aan die aantal vrugte tegelyk beskikbaar op 'n plant, die vrugmorfologie en moontlik die vrugkwaliteit.

8. Die tempo van vrugverwydering was die hoogste in T. leendertziae (2,1 vrugte/uur), laer in V. combreticola (1,2 vrugte/uur) en laagste in T. natalitius (0,4 vrugte/uur), wat hoofsaaklik verband hou met die aantal vrugte tegelyk beskikbaar. In T. leendertziae is twee voedingspieke waargeneem, nl. in die oggend en laat in die middag, wat waarskynlik hoofsaaklik die gevolg is van die vermyding van hoë dagtemperature deur die voëls. Vrugte van T. natalitius is teen 'n stadige tempo dwarsdeur die dag gevreet, wat waarskynlik veroorsaak is deur die lae aantal vrugte beskikbaar. Tydens die lente en somer was die patroon in V. combreticola gelyk aan die patroon in T. leendertziae, waarskynlik om dieselfde redes, maar in die winter is die meeste vrugte tussen 10h00 en 16h00 gevreet, vermoedelik omdat ongemak weens hoë temperature nie so 'n belangrike rol speel gedurende die winter nie, en vanweë die korter dae.

9. Drie metodes van hantering van voëlentvrugte is waargeneem. Tydens die belangrikste (en effektiefste) metode wat gebruik word deur die belangrikste voëlentverspreiders, is die saad kort nadat die vrug ingesluk is (gewoonlik binne 'n minuut), opgebring, en daarna aan die tak afgevee. Muisvoëls het voëlentsade in hulle mis uitgeskei waardeur

baie sade op die grond gemors is, maar hierdie metode is waarskynlik belangrik vir langafstand - verspreiding, aangesien die sade langer in die ingewandes bly. Die Swart Mees en die Rooikopwewer het nie die sade ingesluk nie, maar dit op 'n nabye tak geplant en die arillus gevreet. Die sade is gewoonlik op of baie naby aan die ouerplant gedeponeer.

10. Die vrugte van T. leendertziae en V. combreticola is gewoonlik in die finale rooi stadium gevreet, maar dié van T. natalitius meestal in 'n vroeë groen of groenerig-geel stadium, waarskynlik vanweë die lae aantal vrugte van T. natalitius beskikbaar op enige tydstip.

11. Die aantal vrugte wat per keer gevreet is deur die Geelkoptinker, was 1,6 in T. natalitius, 1,9 in T. leendertziae en 3,2 in V. combreticola, en dit was dus omgekeerd eweredig met die grootte van die betrokke sade. Dieselfde patroon is in ander voëls waargeneem, maar die werklike aantal vrugte ingeneem was hoër, omdat die voëls groter was.

12. Die hanteringstyd van voëlentvrugte was die laagste in die Geelkoptinker. Die tyd bestee per vrug (vanaf die insluk tot die opbring van die saad) was in verhouding met die grootte van die saad: ongeveer 60 sek in T. natalitius, ongeveer 37 sek in T. leendertziae en ongeveer 30 sek in V. combreticola. Die aantal vrugte ingeneem per keer het nie die aantal vrugte wat per eenheid tyd hanteer is, beïnvloed nie.

13. Aggressie tussen voëlentvretende voëls is slegs tussen Geelkoptinkers waargeneem. Hulle het mekaar dikwels (maar nie altyd nie) heftig verjaag, wat toon dat hulle 'n territorium verdedig het.

14. 'n Groot deel van die voëlentsade is op die ouerplant of op sy gasheer gedeponeer (53% in T. natalitius, 58% in T. leendertziae en 83% in V. combreticola), wat hoofsaaklik deur die kort terughoudingstyd van die sade veroorsaak is, en hierdie persentasies was direk eweredig aan die duurte van besoeke aan plante van die verskillende voëlentsoorte . Daar is geen verband gevind tussen die afstand van vlugte van die Geelkoptinker weg van die ouerplant af, en die getal bome of voëlentplante met ryp vrugte beskikbaar rondom die gasheerboomnie.

15. Die Geelkoptinker is slegs by drie geleenthede waargeneem om vrugte anders as voëlentvrugte te vreet en tydens Augustus het dit ook op nektar gevoed. Insekte is ook gevreet. Dit skyn of voëlentvrugte die hoofvoedselbron van Geelkoptinkers vorm.

16. Daar is verskille tussen verskillende plantgemeenskappe gevind met betrekking tot die voorkoms van voëls en voëlente. Die C. apiculatum-gemeenskap was die mees afwykende gemeenskap waarskynlik vanwee die betreklike ongunstige omstandighede wat in die gemeenskap heers, wat 'n korter voortplantingsiklus in die Tapinanthus spesies tot gevolg het.

17. Dit is gevind dat 'n noue interafhanklikheid tussen voëlente en die Geelkoptinker bestaan in die Loskopdam-natuurreservaat; die tinker is die belangrikste en doeltreffendste verspreider van voëlentsade, en die voëlente voorsien die tinker van die grootste deel van sy voedsel in die vorm van 'n baie voedingsryke arillus. Die opbringmetode is die doeltreffendste om die sade netjies en onbeskadig op 'n gasheer te plant, maar dit veroorsaak dat relatief baie sade op die ouerplant of sy gasheerplant gedeponeer is, en dus grotendeels vermors is met die oog op verspreiding. Die uitskeidingsmetode, wat onder andere deur die muisvoels gebruik word, is waarskynlik belangriker vir langafstand-verspreiding.

18. Relatiewe verskille in verspreidingstrategieë is tussen die drie voëlentsoorte waargeneem. Dit is hoofsaaklik beïnvloed deur die grootte van die betrokke saad, die aard van die arillus, die vrugseisoen, die aantal vrugte wat tegelyk beskikbaar is, en moontlik die voedingskwaliteit van die arillus. Dit lyk asof T. natalitius die hoogste verspreidingsdoeltreffendheid per saad het, maar dit produseer vermoedelik die minste vrugte. Die laagste verspreidingsdoeltreffendheid per saad kom voor in V. combreticola, maar hierdie spesie produseer beslis die meeste vrugte.

19. Tinkers is waarskynlik die belangrikste voëlentverspreiders in Afrika in dié gebiede waar dit voorkom. Daar is egter 'n paar gebiede, hoofsaaklik die westelike deel van Suidelike Afrika, waar voëlente voorkom, maar geen tinkers nie, en waar ander voëls dus verantwoordelik is vir die verspreiding van voëlente.

20. Dit lyk of die savanna-bewonende tinkers meer afhanklik van voëlentvrugte is as woud-bewonende soorte, maar alle tinkers gee waarskynlik voorkeur aan voëlentvrugte as dit beskikbaar is.

21. Hoewel die basiese patrone van voëlentverspreiding in die savanna by Loskopdam en in die kusduinewoud in Natal soortgelyk was, is daar enkele verskille. Die belangrikste verskil is dat Swartkoptinkers P. bilineatus (die hoofverspreiders in die woud) ook baie ander vrugte vreet, maar waarskynlik voëlent verkies as dit beskikbaar is en verder laat hulle 35% van die sade grondtoe val, terwyl die Geelkoptinker omtrent elke saad op 'n tak plant. Die Swartkoptinker bring voëlentsade na 'n langer tyd as die

Geelkoptinker op, wat tot gevolg het dat meer sade van die ouerplant weggedra word.

22. In die gematigde streke vreet 'n wye verskeidenheid van voëls voëlentvrugte, hoewel party voëls relatief belangriker vir verspreiding van voëlente is, maar dit lyk of nie een spesiaal aangepas is vir hierdie dieet nie. In elk van die drie tropiese streke kom 'n groep "voëlentspesialiste" voor, wat aangepas is vir hierdie dieet, en wat tot 'n groot mate afhanklik van voëlentvrugte is, wanneer dit beskikbaar is.

23. In die Australo-Orientale gebied is Dicaeum spesies die voëlentspesialiste, wat voël-ente sowel bestuif (hoewel nie net hulle nie) en versprei. Hulle spiermaag is 'n blinde sak wat net insekvoedsel ontvang, en voëlentsade gaan direk deur na die ingewande, sodat die sade vir slegs 'n kort tydjie (dikwels minder as 10 min) in die voël se liggaam verkeer. Die voëls se gedrag tydens uitskeiding verseker dat meeste van die sade aan 'n tak "vasgelym" word.

24. In die Afrotropiese streek is die tinkers die belangrikste verspreiders van voëlentsade, en hulle gewoonte om die sade op te bring en dan aan 'n tak af te vee, is hoogs effektief vir die verspreiding en planting van voëlentsade.

25. In die Neotropiese streek bestaan die euphonias (Euphonia spesies) hoofsaaklik op voëlentvrugte en is die hoofverspreiders daarvan. Hulle het nie 'n spiermaag nie en hulle spysverteringskanaal is "net 'n buis" met 'n uitrekbare deel tussen die proventriculus en die duodenum, wat vinnige deurgang van voëlentsade vergemaklik.

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* = quoted but original not seen

APPENDICES 1 - 8

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APPENDIX 1. CLASSIFICATION OF SOUTHERN AFRICAN (EXCLUDING RHODESIA) MISTLETOES, BASED ON WIENS (1978) AND WIENS (IN PRESS, FLORA OF SOUTHERN AFRICA 10 (1))

Loranthaceae *sensu lato* separated into Loranthaceae *sensu stricto* and Viscaceae

Family Loranthaceae *s. s.* (all species formerly *Loranthus*; specific names have not been changed unless otherwise stated)

Genus *Actinanthella* S. Balle

A. wyliei (Sprague) Wiens

Genus *Erianthemum* v. Tieghem

E. dregei (Eckl. & Zeyh.) v. Tieghem

E. ngamicum (Sprague) Danser

Genus *Helixanthera* Lour.

H. garciana (Engl.) Danser

H. subcylindrica (Sprague) Danser

H. woodii (Engl. & Kr.) Danser

Genus *Moquiniella* S. Balle

M. rubra (Spreng. f.) S. Balle

Genus *Odontella* v. Tieghem

O. welwitschii (Engl.) S. Balle

Genus *Pedistylis* Wiens (cf. Wiens 1978)

P. galpinii (Schinz ex Sprague) Wiens

Genus *Plicosepalus* v. Tieghem

P. amplexicaulis Wiens (cf. Wiens 1978)

P. kalachariensis (Schinz) Danser

P. sagittifolius Sprague

P. undulatus (E. Mey. ex Harv.) v. Tieghem

Genus Septulina v. Tieghem

S. glauca (Thunb.) v. Tieghem

S. ovalis (E. Mey. ex Harv.) v. Tieghem

Genus Tapinanthus Blume

T. carsonii (Bak. & Sprague) Danser

T. cecilae (N. E. Br.) Danser

T. cinereus (Engl.) Danser

T. crassifolius Wiens (cf. Wiens 1978)

T. discolor (Schinz) Danser

T. forbesii (Sprague) Wiens (formerly L. oleifolius var. forbesii, cf. Wiens 1978)

T. glaucocarpus (Peyr.) Danser

T. guerichiii (Engl.) Danser

T. kraussianus ssp. kraussianus (Meisn.) v. Tieghem

ssp. transvaalensis (Sprague) Wiens

T. leendertziae (Sprague) Wiens (formerly L. oleifolius var. leendertziae, cf. Wiens 1978)

T. lugardii (N. E. Br.) Danser

T. minor (Sprague) Danser

T. mollissimus (Engl.) Danser

T. natalitius ssp. natalitius (Meisn.) Danser

ssp. zeyheri (Harv.) Wiens (formerly L. zeyheri, cf. Wiens 1978)

T. oleifolius (Wendl.) Danser

T. prunifolius (E. Mey.) v. Tieghem

T. rubromarginatus (Engl.) Danser

T. sambesiacus (Engl. & Schinz) Danser

T. terminaliae (Engl. & Gilg.) Danser

Genus Tieghemia S. Balle

T. bolusii (Sprague) Wiens

T. quinquenervia (Hochst.) S. Balle

T. rogersii (Burtt Davy) Wiens

Genus Vanwykia Wiens (cf. Wiens 1978)

V. remota (Baker & Sprague) Wiens

Family Viscaceae

Genus Viscum L.

V. anceps E. Mey. ex Sprague

V. capense ssp. capense L.f. (incl. V. robustum Eckl. & Zeyh.)

ssp. hoolei Wiens (cf. Wiens 1978)

V. combreticola Engl.

V. continuum E.Mey. ex Sprague

V. crassulae Eckl. & Zeyh.

V. menyharthii Engl. & Schinz (incl. V. rigidum Engl. & Kr.)

V. minimum Harv.

V. nervosum Hochst. ex A. Rich.

V. obovatum Harv. (incl. V. pulchellum Sprague)

V. obscurum Thunb.

V. oreophilum Wiens (cf. Wiens 1978)

V. pauciflorum L.f. (incl. V. eucleae Eckl. & Zeyh.)

V. rotundifolium L.f. (incl. V. tricostatum E. Mey. and V. thymifolium Presl.)

V. schaeferi Engl. & Kr.

V. spragueanum Burtt Davy

V. subserratum Schlecht.

V. verrucosum Harv.

APPENDIX 2. PHENOLOGICAL NOTES ON ERIANTHEMUM NGAMICUM AND VISCUM ROTUNDIFOLIUM

Erianthemum ngamicum

Occasional observations were made on this species, including a limited number of plants scattered in the N. E. V. (see Section 3.1). Leaf buds first appeared in August. Yellowish flowers appeared in the second half of September, and towards the end of October many flowers, including some already open, were present. Green fruit was observed in January, when all flowers had disappeared. The Yellow-fronted Tinker Barbet was observed eating green fruit on 30 January 1978, when deposited seeds, some already germinating, were noted as well. A single green fruit was observed on 24 February 1977. No flowers or fruit were observed during March, when most leaves had disappeared. Thus, it seems that the reproductive cycle of this mistletoe species starts at about the same time as that of the two Tapinanthus species, but that ripe fruit is formed earlier. The whole cycle appears to last about 22 weeks.

Viscum rotundifolium

Occasional observations were made on this species, mainly in the camp where it occurred in fair numbers. This evergreen plant did not produce all phenological stages continuously like V. combreticola, but at least one of the stages was present at any one time. Flowers started to appear during June and lasted until February. Unripe fruit was formed during December and was predominant during January, though some was still present in July. Ripe fruit appeared in February and was very abundant until June, after which it decreased, with the last ones disappearing in September. Ripe fruit of V. rotundifolium was thus available for a period of eight months, including the winter.

APPENDIX 3. NUMBER OF MONTHLY RECORDS OF BIRDS FEEDING ON FRUIT OF THREE MISTLETOE SPECIES IN SEVEN PLANT COMMUNITIES IN THE LOSKOP DAM NATURE RESERVE DURING MARCH 1977 - APRIL 1978 (APRIL 1977 EXCLUDED)

Observations were made on: Tapinanthus leendertziae (T.l.) during March 1977 and February - April 1978; T. natalitius (T.n.) during March - June 1977 and March - April 1978; Viscum combreticola (V.c.) during May 1977 - April 1978. Months outside these periods are marked "-" in the table below. Observations in the A. caffra - F. saligna community were not possible from September 1977 onwards (marked "rb" in the table below.)

Redfaced Mousebird

T. leendertziae

A. caffra: March 1978 5 records

A. caffra - F. saligna: March 1977 21 records

V. combreticola

Camp: January 4 records

A. caffra - C. apiculatum: March 1977 occasional record

A. caffra: January 10 records

A. caffra - F. saligna: March 1977 occasional record

Blackcollared Barbet

T. leendertziae

Camp: April 1978 4 records

A. caffra: March 1977 2 records, February 2 records

A. karroo: March 1977 6 records, March 1978 4 records

Burkea: March 1977 occasional record

T. natalitius

A. caffra: April 1978 1 record

Burkea: April 1978 3 records

V. combreticola

A. caffra: January 3 records

Burkea: May 4 records, January 4 records, March 1978 4 records

Pied Barbet

T. leendertziae

A. caffra - C. apiculatum: March 1977 14 records, February 4 records

A. karroo: March 1977 1 record

T. natalitius

A. caffra - C. apiculatum: May 3 records, April 1978 2 records

V. combreticola

A. caffra - C. apiculatum: October 4 records, February 3 records

Southern Black Tit

T. leendertziae

A. caffra - C. apiculatum: March 1977 25 records, February 1 record

C. apiculatum: March 1978 3 records

A. caffra - F. saligna: March 1977 3 records

T. natalitius

A. caffra - C. apiculatum: March 1977 8 records

V. combreticola

A. karroo: August 1 record

Plumcoloured Starling

T. leendertziae

Camp: March 1978 5 records

A. caffra - C. apiculatum: March 1977 28 records, March 1978 3 records

A. caffra - F. saligna: March 1977 1 record

Redheaded Weaver

T. leendertziae

A. caffra: March 1977 14 records

Yellowfronted Tinker Barbet

Plant community	Mistletoe	March	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	Sub-total	Grand total
Camp	T.l.	5	-	-	-	-	-	-	-	-	-	0	19	11	35	
	T.n.	4	0	8	-	-	-	-	-	-	-	-	0	8	20	
	V.c.	-	0	0	6	31	7	0	21	17	7	5	0	0	94	149
A. caffra - C. apiculatum	T.l.	68	-	-	-	-	-	-	-	-	-	8	15	9	100	
	T.n.	5	4	0	-	-	-	-	-	-	-	-	5	3	17	
	V.c.	-	4	0	17	19	13	19	0	0	0	3	10	8	93	210
A. caffra	T.l.	3	-	-	-	-	-	-	-	-	-	18	12	0	33	
	T.n.	0	4	0	-	-	-	-	-	-	-	-	2	1	7	
	V.c.	-	4	8	2	0	67	24	0	0	7	11	4	4	131	171
A. karroo	T.l.	11	-	-	-	-	-	-	-	-	-	0	18	0	29	
	T.n.	0	0	2	-	-	-	-	-	-	-	-	3	4	9	
	V.c.	-	0	4	14	13	0	0	0	12	19	4	10	9	67	105
C. apiculatum	T.l.	0	-	-	-	-	-	-	-	-	-	13	13	0	26	
	V.c.	-	0	0	25	17	33	18	0	12	18	10	5	3	151	177
Burkea	T.l.	22	-	-	-	-	-	-	-	-	-	0	0	0	22	
	T.n.	0	0	0	-	-	-	-	-	-	-	-	1	2	3	
	V.c.	-	0	0	2	42	5	8	0	19	3	0	0	3	90	115
A. caffra - F. saligna	T.l.	18	-	-	-	-	rb	rb	rb	rb	rb	rb	rb	rb	18	
	T.n.	6	5	1	-	-	rb	rb	rb	rb	rb	rb	rb	rb	12	
	V.c.	-	0	2	0	0	rb	rb	rb	rb	rb	rb	rb	rb	2	32
Sub-total	T.l.	127	-	-	-	-	-	-	-	-	-	53	63	20	263	
	T.n.	15	13	11	-	-	-	-	-	-	-	-	11	18	68	
	V.c.	-	8	14	66	122	125	69	21	60	54	33	29	27	628	
Grand total		142	21	25	66	122	125	69	21	60	54	86	103	65		959

APPENDIX 4. ALL SOUTHERN AFRICAN RECORDS, I WAS ABLE TO OBTAIN, OF BIRDS EATING MISTLETOE FRUIT

Bird species	Mistletoe [1]	Loranthus [1]	Erianthemum dregei	E. ngamicum	Tapinanthus kraussianus	T. leendertziae	T. natalitius ssp. zeyheri	Viscum [1]	V. capense	V. combreticola	V. obscurum	V. rotundifolium	V. verrucosum	V. "zeyheri"
Knysna Loerie Tauraco corythaix									X		X	X		
Grey Loerie Crinifer concolor								X						
Speckled Mousebird Colius striatus												X		
Whitebacked Mousebird C. colius								X						
Redfaced Mousebird C. indicus						X				X		X		
Grey Hornbill Tockus nasutus		X												
Redbilled Hornbill T. erythrorhynchus		X												
Yellowbilled Hornbill T. flavirostris		X												
Blackcollared Barbet Lybius torquatus						X	X			X				
Pied Barbet L. leucomelas						X	X			X				
Redfronted Tinker Barbet Pogoniulus pusillus			X		X							X	X	
Yellowfronted Tinker Barbet P. chrysoconus				X		X	X			X		X		X
Goldenrumped Tinker Barbet P. bilineatus			X											
Crested Barbet Trachyphonus vaillantii												X		
Southern Black Tit Parus niger						X	X			X				
Cape Bulbul Pycnonotus capensis									X					
Blackeyed Bulbul P. barbatus												X		
Sombre Bulbul Andropadus importunus									X					
Groundscraper Thrush Turdus litsitsirupa								X						
Plumcoloured Starling Cinnyricinclus leucogaster						X	X	X						
Cape Sparrow Passer melanurus								X						
Redheaded Weaver Anaplectes rubriceps						X								
Masked Weaver Ploceus velatus												X		
Streakyheaded Seedeater Serinus gularis								X						
Blackeared Seedeater S. mennelli	X													

PTO

1 = botanical species not stated in source (not marked if a specific record was available)

Sources : Evans 1895; Wood & Evans 1899; Phillips 1928; Skead 1960; Anon. 1962, 1963a, 1963b; Liversidge 1965, 1972; Rowan 1967; Morse-Jones MS; pers. comm. P.G.H. Frost, Mrs. M.K. Rowan; in litt. L.J. Bunning, J. Culverwell, Dr. A.C. Kemp; pers. obs.

APPENDIX 5. COLOUR PREFERENCE EXPERIMENTS WITH A CRESTED BARBET

The Crested Barbet used in the experiments was at first fed minced, raw meat (beef) and later Pro Nutro and apple pieces. It was obtained as a nestling in August 1976, and thus had not been exposed to mistletoe fruit, except for a few fruits of T. leendertziae which I gave it in March 1977. It tried to eat these fruits, but could not swallow them.

In May 1977, I carried out a limited number of colour preference tests with this bird. It was presented with three ripe fruits of T. natalitius simultaneously on a white background: one red, one yellow and one green. The fruits were of similar size. This was repeated three times. In all three trials the bird first handled the green fruit, subsequently the yellow one and last the red one. It had difficulties in handling the fruit and only the seed and aril of the first two, the green and yellow fruits in the first trial, were eventually swallowed.

In June 1977 I carried out two trials, using V. combreticola fruit: one green (unripe), one yellowish (maturing) and one red (fully mature), given simultaneously. In the first trial the bird handled the fruits in the sequence: green, yellowish and red. The green fruit was too hard and was dropped after a while. The yellowish fruit was swallowed after the bird tried to separate the seed and the exocarp. The red fruit was swallowed entirely. In the second trial the red fruit was tackled first, followed by the yellowish one. The green fruit was not touched.

The bird's behaviour in the second and third trials with T. natalitius fruit and in the second trial with V. combreticola fruit can possibly be explained as the result of learning experience. In these trials the bird responded to the differently coloured fruit in sequence of ease of handling, presumably based on learning experience from the first trial. It is difficult, however, to explain why the bird initially responded positively to green fruit, since Turček (1963) showed experimentally that 156 species of European fruit- and seed-eating birds ate more red diaspores and fewer green and yellow ones than could be expected by chance. Nectar-eating hummingbirds (family Trochilidae) appear to have no intrinsic preference for red flowers, but they learn to recognize the colour as a signal of "good" food resources (Grant 1966; Grant &

Grant 1968, quoted by Raven 1972). It may therefore be that colour preference is the result of a learning process in fruit-eating birds, too, possibly illustrated by the Crested Barbet's sequence of responses in the second and third trials of my experiment. Since the experimental bird had been obtained as a nestling, it had had no experience of fruit-eating in nature and thus may not have had an opportunity of learning to associate colour with the food value of fruit. Moreover, it should be kept in mind that only a few trials were carried out on one individual bird and that its apparent preference for green fruit may have been no more than an individual aberration. In this connection, I observed that among other Crested Barbets which I had in captivity, one refused to eat fruit of V.rotundifolium, whereas another three individuals readily ate these fruit (Godschalk 1976).

APPENDIX 6. FRUIT-EATING BIRDS RECORDED IN THE LOSKOP DAM NATURE RESERVE WHICH WERE NOT OBSERVED EATING MISTLETOE FRUIT

Table 9 summarizes the records which are qualified further below.

The Redeyed Turtle Dove was never observed in close association with mistletoe plants. I once disturbed a Green Pigeon from a T. leendertziae plant with ripe fruit. From the bird's behaviour, I suspected it to have eaten the fruit but I did not actually observe this. Green Pigeons were attracted in fair numbers to the camp, because of the presence of many Ficus trees. Two Grey Loeries were observed perched on a large V. combreticola plant with ripe fruit, but showed no intention of eating the fruit. This bird has been recorded eating Viscum fruit (Anon. 1962). Grey and Yellowbilled hornbills were not observed eating mistletoe fruit, though a Grey Hornbill once visited the host of a large number of V. combreticola plants bearing ripe fruit. Grey, Yellowbilled and Redbilled (Tockus erythrorhynchus) hornbills were noted by Kemp (in litt. 1976) to have fed red Loranthus fruit to their nestlings in the Kruger National Park. He could not confirm whether the fruit were actually eaten. The Crested Barbet was once seen close to a T. leendertziae plant with ripe fruit, wiping its bill and flying off. Very close to where it had been perching, a shining, apparently recently deposited seed of T. leendertziae was seen. On two occasions a Crested Barbet was seen visiting a Combretum apiculatum full of V. combreticola plants with many unripe fruit and a few ripe fruit, calling for a while and moving on without showing any intention of eating the fruit. As mentioned earlier, Bunning (in litt. 1977) observed Crested Barbets eating V. rotundifolium fruit. Captive Crested Barbets ate fruit of T. natalitius, V. combreticola and V. rotundifolium (Godschalk 1976, and this study). A female Black Cuckooshrike once moved through a C. apiculatum tree with V. combreticola bearing a few ripe fruit and subsequently through a Sclerocarya caffra with E. ngamicum bearing ripe fruit, but it showed no interest in the fruit. A Blackheaded Oriole was once observed perched at a V. rotundifolium plant with ripe fruit but it did not eat the fruit. Flocks of Arrowmarked Babblers were seen regularly, but they normally moved close to the ground, and were never seen in the immediate vicinity of mistletoes. They were observed to feed regularly on berries of Lantana camara. The most abundant frugivore in the reserve was the Blackeyed Bulbul. This "always-active" bird was, however, never observed eating mistletoe fruit and apparently showed no interest in them all, though Bunning (*in litt.* 1977) recorded Blackeyed Bulbuls eating *V. rotundifolium* fruit and Vaughan (1929) found this bird to be fond of *Loranthus* fruit in Zanzibar. I found captive Blackeyed Bulbuls to be very fond of *V. rotundifolium* fruit, but they refused fruit of *T. natalitius* ssp. *zeyheri* (Godschalk 1976). The Kurrichane Thrush was observed regularly but, as it is mainly a ground feeder, never in close association with mistletoes. The Titbabbler was very uncommon. I once observed it hunting insects in a *V. combreticola* plant with ripe fruit. Twice a pair of Cape Glossy Starlings was observed perched on a *V. combreticola* plant bearing ripe fruit, but they showed no intention of eating the fruit. Redwinged Starlings moved through the study area but never close to mistletoes. The widespread Cape White-eye never took mistletoe fruit, probably because the fruit are rather large and tough for this small, tiny-billed bird, except those of *V. rotundifolium* of which it took fruit rather unwillingly in captivity (Godschalk 1976). The Spottedbacked Weaver *Ploceus cucullatus* was not observed in the reserve, but a large breeding colony was found along the Olifants River. The birds of this colony were observed to feed on fruit of *Ficus natalensis*. The Cape Weaver was never observed very close to mistletoes and was recorded only a few times in the study area. The Masked Weaver, abundant in the camp, was never observed feeding on mistletoe fruit. This bird has been recorded eating *Viscum* fruit (Anon. 1963b) and I observed a member of this species eating *V. rotundifolium* fruit near Hartebeespoort Dam, Transvaal (Godschalk 1976). The Yelloweye Canary was fairly common but was never observed eating mistletoe fruit. I observed it feeding on fruit of *Ficus capensis* and *Lantana rugosa*.

APPENDIX 7. "HANDLING TIME" FOR MISTLETOE FRUIT BY SOME CAPTIVE BIRDS

A captive Yellowfronted Tinker Barbet took 29 sec to eat three fruits of T. leendertziae (at intervals of 6 and 13 sec); after 103 sec it started to regurgitate the seeds at intervals of 67 and 45 sec (a handling time of 78 sec/fruit). On another occasion it regurgitated a seed of the same mistletoe species 134 sec after swallowing it. Another tinker barbet (which was, however, not in a healthy state, and died soon afterwards) once regurgitated a seed of V. combreticola 90 sec after swallowing it. Later it took 30 sec (intervals of 16 and 14 sec) to swallow three fruits of V. combreticola; after 82 sec it started to regurgitate the seeds at intervals of 2,5 and 7 min (a handling time of 227 sec/fruit).

On two occasions a Blackcollared Barbet regurgitated seeds of T. natalitius after 188 and 275 sec, respectively, of having swallowed them. Once it consumed seven fruits of V. combreticola in 120 sec (a mean interval of 20 sec (7-35; n=6); after 243 sec it regurgitated one seed and a second one after another 205 sec; the other seeds were defaecated. On another occasion, it started to regurgitate three seeds 180 sec after swallowing five fruits of V. combreticola, at intervals of 383 and 312 sec, whereas the remaining two seeds were defaecated. One seed out of seven fruits of V. rotundifolium was regurgitated 2-8 min after swallowing, while the remaining seeds were defaecated. By comparison, one seed of Euclea crispa was regurgitated 150 sec after swallowing, while other seeds were defaecated by the Blackcollared Barbet.

A Crested Barbet swallowed two fruits of T. natalitius at an interval of 215 sec, and started to regurgitate the seeds after 220 sec at an interval of 95 sec (a handling time of about 4,5 min/fruit). Two seeds of Euclea crispa were regurgitated 12,5 and 21,5 min, respectively, after being swallowed by this barbet species.

APPENDIX 8 A BRIEF ACCOUNT OF ALL POGONIULUS SPECIES (BASED ON GOODWIN & CLANCEY 1978)

P. duchaillui - Yellowspotted Barbet
habitat : lowland forest (also plantations)
distribution : Central and West Africa

P. olivaceus - Green Barbet
habitat : lowland and highland forest
distribution : highly disjunct in eastern Africa, one race in Ngoye Forest, Zululand

P. scolopaceus - Speckled Tinker Barbet
habitat : fairly wide tolerance, though mainly lowland and gallery forest and somewhat in savanna woodland (also thickets, plantations and partly-cleared cultivated areas)
distribution : Central and West Africa

P. simplex - Green Tinker Barbet
habitat : lowland forest
distribution : East Africa, fairly disjunct populations, including one in Mozambique

P. leucomystax - Moustached Green Tinker Barbet
habitat : montane forest
distribution : East Africa

P. coryphaeus - Western Green Tinker Barbet
habitat : highland forest
distribution : three highly disjunct populations on the south-western, north-western and eastern margins of Central Africa

P. pusillus - Redfronted Tinker Barbet
habitat : in southern Africa evergreen forest edge, riparian woodland and moist wooded savanna; in north-eastern Africa more arid country
distribution : highly disjunct, south-eastern Africa (mainly Natal, eastern Cape) and more widely in north-eastern Africa

P. chrysoconus - Yellowfronted Tinker Barbet

habitat : relatively open and dry savanna, but more humid in north-eastern Africa

distribution : most widespread tinker barbet, all over Africa south of Sahara except central lowland forest area, north-eastern Somaliland, western and southern part of southern Africa

P.S.: The Redfronted and Yellowfronted tinker barbets apparently have reversed habitat preferences in southern and north-eastern Africa

P. subsulphureus - Yellowthroated Tinker Barbet

habitat : humid lowland forest

distribution : Central and West Africa

P. bilineatus - Goldenrumped Tinker Barbet

habitat : mainly forest (also heavy woodland)

distribution : East and South-East Africa

P. leucolaima - Lemonrumped Tinker Barbet

habitat : lowland forest and moist woodland

distribution : Central and West Africa

P. makawai - Whitechested Tinker Barbet

habitat : woodland

distribution : only known from one specimen from north-western Zambia

P. atroflavus - Redrumped Tinker Barbet

habitat : mainly lowland forest

distribution : Central and West Africa